1     Title: A summary of intraspecific size variation for large mysticetes

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Abstract

Following existing work on odontocetes, an extensive survey of literature was conducted to

summarize the growth and body mass of nine mysticete species along with analyses of adult size

distributions using data from the International Whaling Commission catch database.

Relationships uncovered between adult length parameters in mysticetes are combined with

results previously obtained for odontocetes. On average, the mean adult length was 4% below the

asymptotic size and its relative variation appeared to be very similar across most species (CV=4-

5%), though is notably higher in species with more prolonged growth throughout adulthood

(CV=6-8%). Total body mass relationships between mysticete species appear to align with

feeding strategies, as generalists and skim-feeders are notably heavier than lunge-feeding

specialists.

40 1| Introduction

Knowledge on adult size variation in cetaceans can have various applications in the research on

cetacean ecology (Pershing et al., 2010), conservation (Christiansen et al., 2020), stock divisions

(Best, 1977; Ichihara, 1966; Pastene et al., 2020), and evolution (Bianucci et al., 2019; Bisconti

et al., 2021). Due to the broader focus across multiple taxa, one review was only able to examine

the literature and commercial data for *Balaenoptera musculus* (McClain et al., 2015). Since then,

independent advances were made for other species (Agbayani et al., 2020; Christiansen et al.,

2022; Fortune et al., 2021; George et al., 2021; Russell et al., 2023), warranting a deeper review

of existing patterns in adult size variation and body mass relationships.

A comprehensive effort was placed into reviewing the adult variation in total body length (TBL)

and body mass relationships of large cetaceans, beginning with odontocetes (McClure, 2024).

However, the limited number of sampled species prevented strong conclusions. The previous

analysis will now be extended towards nine mysticete species spanning five genera. The

mysticetes selected include all extant members of the Balaenidae family, *Eschrichtius robustus*

(Lilljeborg, 1861), *Megaptera novaeangliae* (Borowski, 1781), and the *Balaenoptera* species

ranging in size from *B. edeni* (Anderson, 1878) to *B. musculus* (Linneaus, 1758).

In general, large baleen whales are weaned within one year, sexually mature after 5-10 years, and

physically mature after 25-40 years (Agbayani et al., 2020; Aguilar & Lockyer, 1987; Bando,

2021; Best, 2011; Best & Lockyer, 2002; Branch, 2008; Chittleborough, 1965; Fortune et al.,

2021). In *Balaena mysticetus* (Linneaus, 1758), sexual maturity occurs after 25 years and

physical growth progresses much further into senescence (George et al., 1999; Tarpley et al.,

2021). As done in the previous analysis (McClure, 2024), the correlation between the interval

from sexual to physical maturity and the coefficients of variation (CV) in mean adult size will be

examined for each species.

An unprecedented review of existing literature was conducted along with an analysis of length

distributions within the IWC catch database. Analyses on body mass relationships, largest

reliable sizes, and postnatal growth are also provided. The data presented in this review will

assist future ecological, anatomical, energetic, and phylogenetic research that benefits from

incorporating intraspecific information about TBL and body mass.

2| Methods

The nine mysticete species under review are summarized in Table 1. Literature was

comprehensively surveyed for morphometric data and growth parameters using the exact

standards described in the previous review for odontocetes (McClure, 2024). Data on the mean

TBL at birth (L_b), weaning (L_w), sexual maturity (L_{sm}), and physical maturity (L_∞) are

summarized here. In total, 332 sources from literature (71 books, 26 conference papers, 224

published articles, 8 technical reports/research documents, 2 theses, and 1 media article) were

surveyed and 125 were selected after filtering.

Most of the published mass data for large mysticetes were the sums of individual pieces weighed

on platform scales or bulk fillings of pressure cookers (Lockyer, 1976). Blood and other body

fluids are lost in this process, typically estimated to compose 6-7% of the total body mass

(Laurie, 1933; Moore et al., 2004). The canonical allometric formula (Equations 1 & 2) and the

Rice-Wolman (RW) model (Equation 3) are reported for mass relationships (George, 2009; Rice

& Wolman, 1971; Schultz, 1938). Formulas, data, references, and code are provided in

Supplementary Files 1-4, respectively.

$$\log(\text{Mass}) = b \times \log(\text{TBL}) + \log(a) \, , (1)$$

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$$\text{Mass} = a \times (\text{TBL})^b , (2)$$

93
$$\text{Mass} = a \times (\text{TBL})^{b1} \times (\text{Girth})^{b2} , (3)$$

As in the analysis for odontocetes (McClure, 2024), the mean adult TBL (L_{mean}) and standard

deviation (SD) of females were primarily estimated using direct samples of individuals recorded

as sexually mature in the commercial data. Corresponding parameters for males were estimated

by dissecting length frequencies of mature individuals from normal probability plots (Harding,

1949). To enforce objectivity and consistency, published estimates for the L_{sm} were used as

starting values for the point of inflection. Preliminary comparisons for select female catches

validated the congruency between the two methods. Therefore, the graphical analysis was

applied to certain female catches where the difference in sample size deemed it preferrable.

Regional differences in the L_{mean} values were examined using two-sample t-tests (Zar, 2010).

The analyses for rorqual species within in the IWC catch database are restricted to expeditions

from after the introduction of minimum length regulations in 1937, corresponding to the ''Late

period'' as described in previous work on *B. musculus* (Branch et al., 2007). This convention

helps minimize data quality issues within early whaling data such as non-standard measuring

techniques, visual estimation, and rounding to 5-ft intervals (Branch et al., 2007; Donovan,

2000). While the intentional 'stretching' of whales below the minimum legal size is known to

afflict much of the data reported prior to the IOS (Best, 1989), these size restrictions had minimal

overlap with the distributions of mature individuals.

The current review distinguishes the three species within *Eubalaena* (Rosenbaum et al., 2000):

E. glacialis in the North Atlantic (Müller, 1776), *E. japonica* in the North Pacific (Lacépède,

1818) and *E. australis* in the Southern Hemisphere (Desmoulins, 1822). Due to limited samples

across both modern catches and necropsies, the adult size for *E. glacilias* was not as deeply

examined. The L_{mean} for *E. australis* and *B. mysticetus* were respectively calculated from the

Soviet commercial catches (Figure S1) and North Pacific subsistence harvests recorded in the

IWC catch database (Figure S2). The L_{mean} for *E. japonica* (Table 2 & Figure S1) were sourced

from sexed individuals from literature (Ivashchenko et al., 2017; Ivashchenko & Clapham, 2012;

Klumov, 1962; Omura et al., 1969; Pike & MacAskie, 1969; Zenkovich, 1954). All non-

examined specimens ≥ 15 m were assumed to be sexually mature. Midpoints were used for

lengths binned to 50 cm intervals.

All stocks within the *B. edeni* complex are treated as one species as the precise taxonomy has yet

to be resolved (Constantine et al., 2018; Junge, 1950). Due to low sample sizes, *B. edeni* catches

from the South Pacific, Southern land stations, and Indian Ocean were excluded from analyses.

Distinct subspecies corresponding to the Northern and Southern Hemispheres are recognized for

nearly all other rorqual species (Jackson et al., 2014; Rice, 1998; Rosel & Wilcox, 2014).

Throughout lower latitudes, the southern populations of *B. musculus* are delineated into *B. m.*

brevicauda (Ichihara, 1966), *B. m. indica* (Blyth, 1859), and another proposed subspecies in

Southeast (SE) Pacific (Attard et al., 2024; Pastene et al., 2020). Each are distinct in size from *B.*

m. intermedia (Burmeister, 1871), the primary subspecies of the Antarctic.

Since mixture within catches would confound regional comparisons, the L_{mean} values for *B.*

musculus in the Southern Hemisphere is summarized in accordance with subspecies rather than

ocean basin. Parameters for mature females from the SE Pacific and the Antarctic were obtained

directly from a previous analysis (Branch et al., 2007). For the graphical analysis of Antarctic

males, whales caught below 60°S were isolated to minimize overlap with other subspecies.

Analyses for *B. m. brevicauda* were restricted to data from Soviet fleets that ignored the 21.3 m

minimum length restriction. Due to known morphological similarities (Branch & Mikhalev,

2008), *B. m. indica* is synonymized with *B. m. brevicauda* in this review.

Since the length distributions for mature mysticetes are approximately normal (Branch et al.,

2007; Ohsumi et al., 1958), the expected upper bound for the maximum value within a normally-

distributed sample of n (Equation 4) is used as an approximation to compare against potentially

unreliable maximum values within the whaling data (Kamath, 2015). For a given

species/subspecies, n is the total number of whales in the entire IWC catch database that were

greater than or equal to the L_{sm} and rounded to the nearest thousand (Y = deviation from mean

TBL).

$$\mathbf{E}\left[Y\right] \leq \sigma \times \sqrt{2 \log n}, (4)$$

155   Since natural variation may enable the occurrence of unexpected outliers, reliable estimates for

156   the L_{max} will also be determined using a combination of the verified measurements in literature

157   and the largest sizes recorded across different expeditions of the total catches within the

158   commercial data. This helps to account for the possible influence of biases in measuring

159   technique.

3| Review of size distributions and mass relationships

163   **Table 1: Summary of adult body length and mass for nine mysticete species.**

Species	Common Name	Mean adult length and mass (M/F)[a,b]	n	Maximum adult length and mass[b]

Species	Common name	Length / Length	Sample size	Length
Eubalaena australis	Southern Right Whale	14.3 m / 14.8 m 46.7 t / 52.0 t	1,341[c] / 551	17.4 m 85.9 t
Eubalaena japonica	North Pacific Right Whale	16.0 m / 16.8 m 66.2 t / 77.1 t	71 / 40	19.7 m 126.4 t
Balaena mysticetus	Bowhead Whale	14.4 m / 15.4 m 47.7 t / 58.8 t	200[c] / 234[c]	20.5 m 172.0 t
Eschrichtius robustus	Gray Whale	12.0 m / 12.6 m 19.1 t / 21.9 t	792[c] / 773[c]	15.2 m 39.3 t
Megaptera novaeangliae	Humpback Whale	12.4 m / 13.3 m 27.7 t / 34.1 t	31,324[c] / 7,237	18.0 m 83.7 t
Balaenoptera edeni	Bryde's Whale	12.6 m / 13.1 m 14.1 t / 15.7 t	6,594[c] / 2,177	16.3 m 28.6 t
Balaenoptera borealis	Sei Whale	14.4 m / 15.4 m 23.1 t / 28.6 t	85,055[c] / 39,843	20.1 m 66.5 t
Balaenoptera physalus	Fin Whale	20.1 m / 21.7 m 51.9 t / 63.0 t	204,370[c] / 99,863	27.2 m 112.1 t
Balaenoptera musculus	Blue Whale	23.6 m / 25.1 m 84.4 t / 103.3 t	34,129[c] / 12,616	31.1 m 209.0 t

a. See text and subsequent tables as some mean lengths are weighted averages for populations with
significant size differences.
b. Body masses are estimated from either linear regression or largest oil yields.
c. Approximate sample size from component curves

Balaenidae

Despite similarity in size between *E. glacilias* and *E. australis* up to sexual maturity

(Christiansen et al., 2022; Fortune et al., 2021), mature females are known to be significantly

larger and in better body condition in the North Atlantic due to environmental stressors

(Christiansen et al., 2020; Stewart et al., 2021). Aside from *E. japonica* being significantly

larger, differences in external morphology between the three species are minimal (Fortune et al.,

2021; Omura et al., 1969). Table 2 shows that the L_{mean} for *E. australis* exceeded the

photogrammetric estimates for the L_∞ (Christiansen et al., 2022). This appears to reflect previous

concerns regarding the compatibility between photogrammetric and commercial data for this

species (Tormosov et al., 1998). This is addressed in greater detail in the discussion.

E. glacialis is sometimes cited to reach a maximum TBL of 17.8-18 m (Cummings, 1985; Huang

et al., 2009), but these measurements were either unstandardized or taken from *E. japonica* when

the two species were still synonymized (Omura, 1958; Thompson, 1928). The largest reliable

measurement in literature for *E. glacialis* was a 16.5 m female captured near Long Island, New

York (Andrews, 1908). The Soviet data for *E. australis* reported males reaching 17.2 m, and the

infraction records for other nations reported a female measuring 17.4 m. The largest reliable

measurements for *E. japonica* appear to be a binned length of 18.1-18.5 m for a male and 19.5-

19.8 m for a female (Ivashchenko & Clapham, 2012).

Table 2: Growth parameters for Balaenidae

Species	L_b (m)	L_w (m)	L_{sm} (m) M/F	$L_{mean} \pm$ SD (m) M/F	L_∞ (m) M/F	L_{max} (m) M/F	Reference
E. japonica	—	11	14.5[a]	16.0 ± 0.86 / 16.8 ± 1.13	16.5[a] / 17.5[a]	18.3[a] / 19.7[a]	Ivashchenko & Clapham, 2012; Klumov, 1962; Omura et al., 1969; Current study
E. australis	4.7	9.5	12.6[b] / 13.1	14.3 ± 0.78[c] / 14.8 ± 0.98[c]	13.7[b] / 14.3	17.2 / 17.4	Christiansen et al., 2022; Current study
B. mysticetus	4.3	8.5	12.7[a] / 13.4	14.4 ± 1.20 / 15.4 ± 1.26[d]	15.5[a] / 16.5[a]	19.2[e] / 20.5[e]	George et al., 1999; Lubetkin et al., 2012; Tarpley et al., 2021; Current study

193   a.   Midpoint of binned value or estimated range in literature.
194   b.   Estimated by adjusting for 4% difference between males and females
195   c.   Whaling data may not be directly comparable to L_∞ values from photogrammetry surveys.
196   d.   Estimated from graphical analysis of total female catch.
197   e.   Estimates from Equation 4.
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For *B. mysticetus*, the largest female and male within the analyzed harvest data were 19.2 m and

17.8 m, respectively. The minimum estimate for the historical population size of the North

Pacific population of *B. mysticetus* is around 13,000 (Woodby & Botkin, 1993). If it's assumed

that mature females composed 25% of this value, Equation 4 predicts the female L_{max} to be 20.5

m. Given the selection against larger individuals in subsistence harvests and the high variability

of continued growth in *B. mysticetus*, Equation 4's prediction is likely the best L_{max} value for this

species.

Postnatal and near-term fetal weights have been published for *E. japonica* (n= 18), *E. glacialis*

(n=13), *E australis* (n=3), and *B. mysticetus* (n=7) from necropsies and whaling (Best, 2008;

Fortune et al., 2021; George, 2009; Klumov, 1962; Omura et al., 1969). The heaviest record for

E. japonica was a 17.4 m lactating female that weighed 106.5 tonnes after flensing or 113.3

tonnes after a 6 % fluid correction (Klumov, 1962). The heaviest RW body mass estimate for *B.*

mysticetus was 101 tonnes for a 16.5 m female (George et al., 2021).

The RW1 body mass model published for *B. mysticetus* (George, 2009) accurately predicted the

masses for the non-pregnant *E. japonica* specimens (r^2= 0.969; n=6), excluding three outliers

with known errors in girth measurements (Christiansen et al., 2019). AIC model selection

preferred a linear model (Equation 1) that pooled the mass data for the two genera (AICc = -

65.98, weight = 0.74). Mass data and external measurements for each species were pooled into

Equations 1-3 as composite models for the Balaenidae family (Table S1, Figures 1 & S3). As

explicitly noted by the original author (Klumov, 1962), corrections on the order of 8-11 tonnes

were necessary for three whales that were missing components for the skulls and viscera. This

went unmentioned when the data was republished in the more widely-cited review (Omura et al.,

1969). Consequently, these underestimated weights remained uncorrected in subsequent

literature (Fortune et al., 2021; Lockyer, 1976).

Figure 1A compares the composite balaenid model (Equation 2) to photogrammetric mass

models for *E. australis* and *B. mysticetus* (Christiansen et al., 2022, 2024). A balaenid would

weigh 54.2 tonnes (80% PI 42.6-69.4 tonnes) at 15 m and 143.0 tonnes (80% PI 111.1-184.2

tonnes) at 20.5 m. Oil yield to body mass conversions for *B. mysticetus* (George et al., 2007,

2021) suggest that individuals yielding 337-375 barrels (37.0-40.9 tonnes) of oil (Fairburn, 1955;

Pease, 1918; Williams, 1904) would have weighed 154-172 tonnes intact. These figures fall well

within the expected body mass for a 20.5 m balaenid.

Eschrichtiidae

For *E. robustus*, the graphical analysis of the total catches was employed for both sexes (Table 3

& Figure S4). The largest canonically cited individuals are a 14.62 m male and a 15.54 m

unsexed specimen (Cope, 1868), though the reliability of these measurements are questionable

(Andrews, 1914). A 14.3 m male and 15 m female were verified by researchers aboard the *Aleut*

(Zenkovich, 1934, 1937). The commercial dataset reports 10 males exceeding 14.3 m and 4

females exceeding 15 m. The largest individual was an 18.3 m male caught in 1928, which is

likely not reliable as there are no records of females exceeding 15.2 m. When accounting for

sexual dimorphism, the largest reliably recorded males in the commercial data appear to be 14.5

m.

247   **Table 3: Growth parameters for *E. robustus***

Length	Males	Females	Reference
L_b (m)	4.6	4.7	Agbayani et al., 2020
L_w (m)	8.3	8.4	Agbayani et al., 2020
L_{sm} (m)	11.1	11.6	Agbayani et al., 2020

$L_{mean} \pm$ **SD**	12.0 ± 0.63	12.5 ± 0.68	Current study
L_∞ (m)	12.6	13.1	Agbayani et al., 2020
L_{max} (m)	14.5	15.2	Current study

In total, 36 weights for *E. robustus* collected from whaling, strandings, and captive specimens

have been published (Agbayani et al., 2020; Sumich et al., 2013). The heaviest was a 13.55 m

pregnant female that weighed 33.85 tonnes after flensing (Rice & Wolman, 1971). The various

published models for this species are provided in Table S2 (Agbayani et al., 2020; Christiansen

et al., 2021; Lockyer, 1976; Sumich, 1986; Sumich et al., 2013). For the RW curves in Figure

1B, girths are fixed to the observed values of 50% of the TBL for the lean condition, 60% for the

standard fattened condition, and 70% for the pregnant fattened condition (Sumich, 1986).

Figure 1B shows that the mass relationship published alongside a recent growth curve (Agbayani

et al., 2020) precisely aligned with both the RW curve for the lean condition and a volume model

for a predominantly emaciated sample of whales (Christiansen et al., 2021). This supports

concerns by the authors (Agbayani et al., 2020) that the sample for this model appears too

limited to represent the normal condition. When setting the RW model at the normal body

condition (girth = 55% TBL), *E. robustus* would weigh 19.1 tonnes at 12 m while a pregnant

female would weigh 39.3 tonnes at 15.2 m.

Balaenopteridae

Growth parameters along with corresponding L_{mean} values are provided in Table 4. Due to

congruity in existing L_{sm} and L_∞ estimates, all *M. novaeangliae* populations and certain

subspecies within *Balaenoptera* were pooled together in Table 4 and supplementary plots

(Figures S5-S17).

Table 4: Growth parameters for Balaenopteridae

Species	L_b (m)	L_w (m)	L_{sm} (m) M/F	$L_{mean} \pm$ SD (m)[a] M/F	L_∞ (m) M/F	L_{max} (m) M/F	Reference
M. novaeangliae	4.3	9.1	11.2 / 11.9	12.4 ± 0.86 / 13.3 ± 0.91	13.1 / 13.7	17.0[b] / 18.0[b]	Chittleborough, 1965; Nishiwaki, 1959, 1960; Current Study
B. edeni (**North Pacific**)	4	7.1[c]	11.4 / 11.8	12.5 ± 0.56 / 13.0 ± 0.55	12.7 / 13.3	14.8 / 15.5	Bando, 2021; Lockyer, 1984; Current Study
B. b. borealis	4.3	9[c]	12.7 / 13.3	13.7 ± 0.61 / 14.5 ± 0.69	14.1 / 15.2	17.5[b] / 18.6	Bando, 2020; Best & Lockyer, 2002; Lockyer, 1984; Current Study
B. b. schlegelii	4.3	8[c]	13.8 / 14.1	14.7 ± 0.62 / 15.6 ± 0.74	15.5[d]/ 16.5[d]	19.0[b]/20.1	Best & Lockyer, 2002; Lockyer, 1977, 1984 Current Study
B. p. physalus / velifera	6.4	11.3	17.4 / 18.5	18.4 ± 0.90 / 19.7 ± 1.00	19.2 / 20.7	23.6 / 25.3	Aguilar et al., 1988; Ohsumi et al., 1958; Current Study
B. p. quoyi	6-6.5	12	19.2 / 20.0	20.4 ± 0.86 / 21.9 ± 1.06	21.0 / 22.3	25.0 / 27.2	Mackintosh, 1942; Mackintosh & Wheeler, 1929; Current Study
B. m. musculus	—	—	20.5 / 21.5	22.8 ± 1.02 / 24.0 ± 1.17	23.4 / 24.8	26.8 / 28.0	Pike & McAskie, 1969; Ohsumi, 1979; Current Study
B. m. intermedia	7	16	22.6 / 23.4	24.0 ± 1.11 / 25.7 ± 1.24[e]	25.0 / 26.2	29.9 / 31.1	Branch & Mikhalev, 2008; Lockyer, 1981;

							Mackintosh & Wheeler, 1929; Current study
B. m. brevicauda	5.6	13.5	18.3 / 19.2	20.0 ± 0.92 / 20.9 ± 1.04	21.1 / 21.9	23.8 / 24.4	Branch, 2008; Ichihara, 1966; Mikhalev, 2019; Current study

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a. Reflects pooled averages for species/group. Sample sizes reported in Table 10.
b. Estimated parameter.
c. Data insufficient or extrapolation.
d. These values correspond to whales captured off South Georgia. Sei whales captured off Donkergat and
Durban were known to physically mature at around 15.8 m and 14.8 m for females and males, respectively.
e. Weighted mean and SD of model estimates for pelagic data (1937-1973).
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For *M. novaeangliae*, adults from the South Atlantic, North Atlantic, and Southern Hemisphere

land stations were significantly larger (*t*-test, $p < 0.05$) than all other regions (Table 5). Equation

4 predicted L_{max} values of 17.5 m (n = 34,000) for females and 16.4 m (n = 44,000) for males.

Since 1937, 17 males and 13 females were reported to measure 17 m or greater. The largest

female was reportedly 19.5 m, while the next 13 were 18.3 m or lower.

The largest record amongst precisely calibrated photogrammetry measurements was a 16.8 m

individual observed repeatedly in the Arabian Sea (F. Christiansen, personal communication,

2023). The mounted skeleton displayed at the Nha Trang Institute of Oceanography in Vietnam

appears to be the largest in the world, officially measuring 18 m (Redman, 2019). When

comparing this to the values from the commercial data and Equation 4's predictions, the L_{max} for

M. novaeangliae can be estimated to be 18 m for females and 17 m for males.

293   **Table 5: Regional comparison of L_{mean} for *M. novaeangliae*.**

L_{mean} ± SD (m)

Region	Males	Females
North Pacific	12.4 ± 0.93 (2,594)	13.2 ± 0.97 (465)
North Atlantic	12.9 ±1.16 (113)	13.7 ± 0.90 (35)
South Pacific	12.4 ± 0.70 (6,008)	13.3 ± 0.74 (433)
South Atlantic	13.1 ± 1.00 (1,805)	14.4 ± 0.93 (62)
Indian Ocean	12.2 ± 0.79 (8,756)	13.3 ± 0.80 (632)
S. Hemisphere Land Stations	12.8 ± 0.78 (178)	13.8 ± 0.91 (61)
S. Hemisphere Pelagic	12.4 ± 0.78 (5,781)	13.2 ± 0.87 (3,455)
S. Hemisphere Pelagic (Soviet)	12.4 ± 1.00 (4,740)	13.3 ± 0.96 (2,097)

For *B. edeni*, the length distributions of mature females in the South Atlantic and Southern

pelagic catches were polymodal (Figures S6 & S7), consistent with observations of distinct

morphs (Best, 1977; Ohsumi, 1980). These distributions were excluded from *t*-test comparisons.

The South Atlantic data contains a peak around 15.5 m and a maximum TBL of 18 m (Figure

S6), indicating that nearly 20% of the sample were misidentified catches of *B. borealis* (Figure

S7). Outliers of this type comprised only a small percentage of the total male catches for the

South Atlantic (< 2.0 %) and North Pacific (< 0.02%). Otherwise, no obvious mixtures of

different morphs or species were detected in other regions (Figures S8 & S9).

Adults from the North Pacific were significantly smaller ($p < 0.05$) than those from the Southern

Hemisphere (Table 6). Due to rampant misidentification with other rorquals, caution should be

taken with commercial records of individuals exceeding 15.5 m, a length typically not exceeded

in verified records (Best, 1977; Ohsumi, 1980). The largest specimen that can be tentatively

assigned to *B. edeni* was a 16.3 m female captured off of Western Australia in 1963 (Best, 1977).

A corresponding record of a 15.9 m male within the Soviet catch data from the Gulf of Aden

seemed particularly convincing, as both the whaling data and lack of confirmed sightings in

literature suggests that sei whales are infrequent or wholly absent in the Arabian Sea region.

Table 6: Regional comparison of L_{mean} for *B. edeni*.

Region	$L_{mean} \pm$ SD (m) (n)	
	Males	**Females**
North Pacific	12.5 ± 0.55 (5,366)	13.0 ± 0.55 (1,724)
South Atlantic	13.2 ± 0.87^{a} (629)	13.7 ± 0.60 [a,b] (121)
S. Hemisphere Pelagic	13.0 ± 0.58 (222)	13.6 ± 0.67^{b} (83)
S. Hemisphere Pelagic (Soviet)	13.1 ± 0.56 (377)	13.6 ± 0.65 (249)

315   a.   *B. borealis* mixture detected within total sample. Reported mean and sample size calculated from isolated
316   components for *B.edeni*.
317   b.   Mixture of two morphs
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The L_{mean} values for *B. borealis* in the Indian Ocean and South Atlantic were significantly lower

(*t*-test, $p < 0.05$) than those from Southern land station and pelagic catches (Table 7). Adults

from the South Pacific were even smaller, falling within the size range of adults from the

Northern Hemisphere. The graphically estimated parameters reported in Table 7 were consistent

with the limited sample of mature females (mean = 14.1 m; SD = 0.76 m; median & mode=14.3

m; $n = 26$). The data from the South Pacific was not used to calculate the L_{mean} for southern sei

whales in Table 4.

The largest female within the total catches for *B. borealis* in the Northern Hemisphere was an

18.6 m individual captured off the North Pacific. The next 13 measured between 17-18 m. The

largest in the Southern Hemisphere were two 20.1 m individuals captured at South Georgia in

1949 and 1960. The next 15 largest measured between 18.3 m-19.6 m. These do not readily

appear to be misidentified records for *B. physalus* when adding some allowance to the Equation

4 predictions of 17.6 m (n = 18,000) for northern females and 19.1 m (n = 67,000) for southern

females. There are questionable records of males exceeding the maximum reported female size.

The L_{max} for males reported in Table 4 were therefore downsized from the largest females using

the ratio of sexual dimorphism of their respective L_∞ values.

Table 7: Regional comparison of L_{mean} for *B. borealis*.

	$L_{mean} \pm$ SD (m)	
Region	**Males**	**Females**
North Pacific	13.7 ± 0.61 (18,588)	14.6 ± 0.68 (6,850)
North Atlantic	13.3 ± 0.65 (1,783)	14.2 ± 0.65 (315)
South Pacific	13.6 ± 0.90 (284)	14.4 ± 0.80[a] (362)
South Atlantic	14.6 ± 0.90 (3,892)	15.0 ± 0.85 (1,145)
Indian Ocean	14.0 ± 0.68 (1,212)	15.0 ± 0.94 (102)
S. Hemisphere Land Stations	14.9 ± 0.55 (4,825)	15.8 ± 0.68 (2,692)

S. Hemisphere Pelagic	14.6 ± 0.59 (42,127)	15.6 ± 0.73 (20,330)
S. Hemisphere Pelagic (Soviet)	14.8 ± 0.65 (13,393)	15.6 ± 0.76 (8,407)

a.   Estimated from graphical analysis of total female catch

Despite possessing similar means (Table 8), the female length distributions for *B. physalus* in the

South Atlantic and Indian Ocean land stations were strongly negatively skewed (Figure S13).

They were thus excluded from *t*-test comparisons. While the distributions for the rest of the

Southern Hemisphere were approximately normal, outliers as small as 14.3-16 m were detected

across the Chilean, Soviet, and British catches. Apart from comparisons between the South

Pacific and Soviet Pelagic female catches, all regional differences in mean length ≥ 0.1 m were

statistically significant (*t*-test, $p < 0.05$).

The Equation 4 predictions for northern and southern females were respectively 24.2 m (n =

29,000) and 27.2 m (n = 220,000). The largest females from the North Pacific and Atlantic

respectively measured 25 and 25.3 m. The Soviet data from the Antarctic records one female

reaching 27.2 m, consistent with Equation 4's prediction. The largest male from the North

Pacific measured 23.6 m, congruent with a stranding record of another male with an approximate

length of 22-24 m (Zhu et al., 2018; "中国最大长须鲸骨骼标本来了 [China's largest fin whale

skeleton specimen arrives]," 2021). A southern male reported to measure 25 m lies close to the

Equation 4 prediction (24.7 m; n = 240,000), whereas two larger individuals were liable to have

been misidentified females.

Table 8: Regional comparison of L_{mean} for *B. physalus*.

	$L_{mean} \pm$ SD (m)	
Region	**Males**	**Females**
North Pacific	18.4 ± 0.89 (16,619)	19.7 ± 0.94 (4,877)
North Atlantic	18.2 ± 1.01 (12,593)	19.6 ± 1.10 (2,446)
South Pacific	20.1 ± 0.78 (142)	21.3 ± 1.00[a] (94)
South Atlantic	19.9 ± 1.19 (666)	21.3 ± 2.07[b] (35)
Indian Ocean	19.9 ± 0.99 (3,169)	21.8 ± 1.47[b] (73)
S. Hemisphere Land Stations	19.9 ± 0.91 (14,564)	21.7 ± 1.14 (3,892)
S. Hemisphere Pelagic	20.4 ± 0.82 (173,095)	21.9 ± 1.05 (85,403)
S. Hemisphere Pelagic (Soviet)	20.1 ± 1.00 (4,828)	21.5 ± 1.19 (3,214)

360   a.   Estimated from graphical analysis of total female catch
361   b.   Negatively skewed.
362

The SE Pacific subspecies of *B. musculus* was very comparable in size to the northern subspecies

(Table 9), though a significant difference was detected between the SE Pacific and North Pacific

(*t*-test, $p < 0.05$). The largest whales reliably identified as *B. m. brevicauda* appear to have been

around 24.2-24.5 m (Omura, 1984; Pastene et al., 2020). The largest individual in the Northern

Hemisphere dataset was a 28.0 m female from the North Atlantic, a size substantiated by

mounted skeletons and photogrammetry studies on the northern subspecies (Gorter, 2010;

Ortega-Ortiz et al., 2022).

While the literature (Risting, 1922, 1928) and commercial data from early Norwegian

expeditions report that *B. m. intermedia* reached 32-35 m, contemporary expeditions by other

nations only reported TBLs up to 31.1 m. The maximum sizes within Norwegian catch statistics

fell in line with other nations after 1931, hinting that at least most of these exceptional records

were artefacts from measuring procedures. The greatest TBL for *B. m. intermedia* to be directly

measured by a scientist was 29.9 m (Rice, 1978). Since 1937, the commercial data reports six

females $\geq$ 30.5 m, the largest was taken in 1948 and measured 31.1 m. This size falls well within

Equation 4's prediction of 31.6 m when conservatively estimating that only 50% of all captured

females in the IWC catch database were mature (n = 77,956).

381   **Table 9: Regional comparison of L_{mean} for *B. musculus*.**

	$L_{mean} \pm SD$ (m)	
Region	**Males**	**Females**
North Pacific	22.8 $\pm$ 0.98 (1,054)	24.1 $\pm$ 1.05 (183)
North Atlantic	22.2 $\pm$ 1.03 (202)	23.4 $\pm$ 1.45 (44)
Antarctic	24.0 $\pm$ 1.11 (28,865)	25.7 $\pm$ 1.24[a] (10,809)
Pygmy	20.0 $\pm$ 0.92 (3,199)	20.9 $\pm$ 1.04 (1,509)
SE Pacific	22.1 $\pm$ 1.13[b] (809)	23.5 $\pm$ 1.20[b] (71)

382
a.   Weighted average of mean and SD of Pelagic catch below 60°S (1937-1973) from Branch et al., 2007.

b.   Includes data taken since 1931.

The heaviest piecemeal masses reported in communications and previous literature were 56.1

tonnes for *M. novaeangliae* (Best, 2008) , 24.9 tonnes for *B. edeni* (Tamura et al., 2016), and

40.45 tonnes for *B. borealis* (Y. Ivashchenko, personal communication, 2023). The heaviest

weight recorded for *B. physalus* was a 21.3 m North Atlantic female that weighed 69.3 tonnes

(Víkingsson et al., 1988), with corrections for the missing tongue and body fluids amounting to

76.4 tonnes. The heaviest record for *B. musculus* was a 27.6 m pregnant female reported to

weigh 190 tonnes (Voronin, 1948). This individual's maximum blubber thickness of 42 cm

substantiates that this individual was of exceptional condition, as this measurement rarely

approaches 40 cm (Slijper, 1948). A record of 196 long tons / 199 tonnes reported in some

literature (Carwardine, 1995; McClain et al., 2015), appears to be a conversion error for a total

mass of 178 tonnes /196 short tons (Scheffer, 1974).

Along with existing formulas (Table S8), individual weights for *M. novaeangliae* (n = 50), *B.*

borealis (n = 60), *B. physalus* (n =106) and *B. musculus* (n = 56) were compiled for this review.

Fluid-corrected body mass data and corresponding curves for Balaenopteridae are compared in

Figures 1C & D. The dataset for *M. novaeangliae* and *B. borealis* were larger than those

available to previous authors (Lockyer, 1976; Mikhalev, 2019) and all data were compiled into

mass models for their respective species (Table S3, Figures 1, S18 & S19). While AIC model

selection strongly preferred separate regional models for *B. borealis* (AICc=-145.32, weight =

1), summary statistics on adult body weight from unpublished JARPNII survey data (Tamura et

al., 2016) strongly hint that previously observed regional differences in weight were due to

temporal sampling bias (Víkingsson et al., 1988).

Figure 1: Body mass relationships for large mysticetes

Legend: Fluid-corrected body mass data for Balaenidae (A), *E. robustus* (B), *M. novaeangliae/B.*

411　　　　　　　　　　　　　*physalus/B. borealis* (C), and *B. musculus* (D).

Skeletal mass regressions for *B. musculus* ($r^2 = 0.910$, $n = 43$) and *B. physalus* ($r^2 = 0.856$, $n =$

40) were coupled with published soft tissue ratios (Lockyer, 1981) to produce mass models

corresponding to the extremes in body conditions (Figures 1, S20, & S21). The ratios for *B.*

physalus were updated with additional data (Mogoe et al., 2014). To account for the observed

discrepancy in the visceral weight (Omura et al., 1970), adjustments in the visceral components

were calculated and refitted into a mass model for *B. m. brevicauda* (Table S3). Figure 1 shows

that all *Balaenoptera* species are considerably lighter than balaenids, *E. robustus*, and *M.*

novaeangliae at equal lengths. With a 6% correction, the regression models predict *B. m.*

brevicauda weighing 96.7 tonnes (77.6-115.8 tonnes) at 24.4 m, *B. m. intermedia* weighing

130.7 tonnes (105.0-156.4 tonnes) at 27 m, and 207.8 tonnes (167.0-248.7 tonnes) at 31.1 m.

While mass data for *B. musculus* is sparse for individuals exceeding 28 m, whalers generally

observed that exceptionally long females produced only slightly more oil than fattened

individuals between 24-27.4 m (Walsh, 2010). The record yield was 354 barrels / 56.64 tonnes

from a 30.8 m pregnant female while 305 barrels / 48.8 tonnes was extracted from a 27.7 m

individual (Tønnessen & Johnsen, 1982). It may be that 27-28 m is the maximum TBL for

optimal weight gain and larger whales cannot become especially fat. Oil yields from blubber,

meat, and bones compose up to 29% of the total piecemeal mass of a fattened individual

(Lockyer, 1981). This predicts an intact body mass of at least 209 tonnes for a whale that

produced 56.64 tonnes of oil.

Relationships between length parameters

The following analyses combined the parameters reported in both the present review and

previous work on odontocetes (McClure, 2024). The relationship between L_b, L_w, and maternal

size were previously investigated using interchangeable use of the female L_∞ and L_{max} (Huang et

al., 2009). This was re-examined using more precise estimates of the female L_∞ and observed

440 values of L_b (n = 13) and L_w (n = 12). On average, L_b equaled 33.6% of L_∞ and was significantly

441 larger in odontocetes (mean = 41.9%, n = 4) than in mysticetes (mean = 29.8%, n = 9, Welch's

442 two-sample t-test: $p < 0.05$). The L_w averaged 63.5 % of L_∞ and the difference between

443 odontocetes (mean = 73.1%, n = 3) and mysticetes (mean =60.3%, n = 9) was not significant

444 (Welch's two-sample t-test, $p > 0.05$).

446     **Table 10: Relationships between L_{sm}, L_{mean}, and L_∞ in large mysticetes.**

Species	L_{sm}/L_{mean} (%) M/F	L_{sm}/L_∞ (%) M/F	L_{mean}/L_∞ (%) M/F	CV (%) M/F	N M/F
E. japonica	90.6 / 86.3	87.9 / 82.9	97.0 / 96.0	5.40 / 6.74	71 / 40
B. mysticetus	88.2 / 87.0	81.9 / 81.2	92.9 / 93.3	8.33 / 8.18	200[a] / 234[a]
E. robustus	92.5 / 92.8	88.1 / 88.5	95.2 / 95.4	5.25 / 5.44	792[a] / 773[a]
M. novaeangliae	90.3 / 89.5	85.5 / 86.9	94.7 / 97.1	6.94 / 6.84	31,324[a] / 7,237
B. edeni (North Pacific)	91.2 / 90.8	89. 9 / 88.7	98.4 / 97.7	4.48 / 4.23	5,047[a] / 1,724
B. borealis North	92.7 / 91.7	90.1 / 87.5	97.2 / 95.4	4.45 / 4.76	20,016[a] / 7,165
South	93.9 / 90.4	89.0 / 86.0	94.8 / 95.1	4.22 / 4.74	65,039[a] / 32,678
B. physalus North	94.1 / 93.9	90.6 / 89.4	96.4 / 95.2	4.86 / 5.08	26,009[a] / 7,323
South	94.1 / 91.3	91.4 / 89.7	97.1 / 98.2	4.22 / 4.84	178,361[a] / 92,631
B. musculus North	90.9 / 90.2	88.6 / 87.3	97.4 / 96.8	4.47 / 4.88	1,147[a] / 227
Antarctic	94.2 / 91.4	90.4 / 89.7	96.0 / 98.1	4.63 / 4.82	28,865[a] / 10,809
Pygmy	91.5 / 91.9	86.7 / 87.7	94.8 /95.4	4.60 / 4.98	3,199[a] / 1,509

447  a. Estimate from component curve.
448

Being parameters for adult size, the relationships between L_{mean}, L_{sm}, and L_∞ are compared in

species and subspecies for which all three were known (Table 10). *E. australis* was omitted due

to issues with the compatibility of the L_∞ estimates from photogrammetry data. On average, the

L_{sm}/L_{mean}, L_{sm}/L_∞, and L_{mean}/L_∞ ratios equaled 87.4%, 90.9%, and 96.0%, respectively. None of

these values were significantly different between odontocetes and mysticetes (Welch's two-

sample *t*-test, $p < 0.05$). After removing species where < 200 mature individuals were sampled,

the species with the highest CV values were *B. mysticetus*, *P. macrocephalus*, and *M.*

novaeangliae. As would be expected, the correlation against CV was statistically significant for

all three ratios: L_{sm}/L_{mean} ($F_{1,24}=23.1$, $p < 0.001$), L_{mean}/L_∞ ($F_{1,24}= 43.1$, $p < 0.001$), and L_{mean}/L_∞

($F_{1,24}= 16.4$, $p < 0.001$).

4| Discussion

The discrepancy between commercial data and photogrammetry measurements for *E. australis*

mirrored previous observations for both this species (Tormosov et al., 1998) and *B. mysticetus*

(George et al., 2004), where hauled whales appeared to be systematically longer. This

phenomenon is replicated to neither the same degree nor consistency in more streamlined species

that overlap in mass (Bierlich et al., 2023; Miller et al., 2013; Ortega-Ortiz et al., 2022; Russell

et al., 2023, 2024). Rather than the tissue itself stretching from the force, the discrepancy appears

to be due to Balaenids experiencing a greater post-mortem deviation from their natural posture

while lying upon a flat surface.

It is notable that the photogrammetric volume models for *B. musculus*, *M. novaeangliae*, *E.*

robustus, P. macrocephalus were able to match the mass models derived from direct weighings

with body density estimates nearer to that of seawater (Christiansen et al., 2021; Glarou et al.,

2022; Napoli et al., 2024; Russell et al., 2023, 2024). By contrast, photogrammetric models for

balaenids predicted notably lower body density estimates (Christiansen et al., 2024; Glarou et al.,

2022). As the true body mass and volume would remain constant as the posture changes, the

volume of landed whales might be overestimated by models designed for photographed whales.

This may introduce downward bias when calculating the average body density of landed whales

by their estimated volume (Christiansen et al., 2019, 2024). Since the compatibility between

commercial and photogrammetry data implies that other species exhibit a straighter natural

posture, measurements for balaenids taken along a flat surface may be more compatible for

interspecies comparisons.

In general, the regional differences in L_{mean} for *Balaenoptera* species were consistent with

previous research that uncovered either inherent differences in asymptotic size (Best, 1977; Best

& Lockyer, 2002; Lockyer, 1977; Ohsumi, 1980) or variation in growth rate (Lockyer, 1981;

Mogoe et al., 2014; Panfilov, 1978). However, differences were also detected for populations

that were considered synonymous in size, such as the northern populations of *B. physalus*

(Aguilar et al., 1988; Aguilar & Lockyer, 1987) and certain populations within *M. novaeangliae*

(Chittleborough, 1965; Stevick, 1999). It may be, as previously concluded for *P. macrocephalus*

(McClure, 2024), that these differences are confounded by age composition or catch selectivity,

negating a true morphological difference. There may also be evidence of density-dependent

growth, as the highest L_{mean} values reported for *M. novaeangliae* belonged to the smallest

catches.

Across the Southern Hemisphere dataset for *B. physalus,* several expeditions reported mature

females as small as 14.3-16 m. This is notable as the smallest mature females reported in

biological studies typically measured 18.5-18.6 m (Kakuwa et al., 1953; Mackintosh, 1942;

Ohno & Fujino, 1952). While unusually small mature females would align with the observations

made for a proposed pygmy subspecies (Clarke, 2004), clerical errors or species

misidentification must also be considered.

For *B. musculus*, the SE Pacific catch was most similar in mean size to the northern subspecies,

in agreement with the results of genetic clustering with the ENP stock (Attard et al., 2024). The

size difference from the pooled North Pacific catch data aligns with previous findings in

separating the ENP and WNP populations (Monnahan et al., 2014). The South Pacific catch for

B. borealis mirrors this trend in body size without any obvious signs of species misidentification

with *B. edeni*. While biological studies do not seem to be available, the calls recorded from *B.*

borealis near Chile were unique from all other regions (Español-Jiménez et al., 2019). This

would support that the SE Pacific stock for *B. borealis* may be a discrete population from the rest

known in the Southern Hemisphere.

Interspecific differences in body mass were notably grouped by feeding strategy: lunge-feeding

Balaenoptera were the lightest and the skim-feeding balaenids were the heaviest by a substantial

margin, as previously acknowledged (George, 2009; Lockyer, 1976). Intermediate of the two

groups were *E. robustus* and *M. novaeangliae*, generalists that employ a combination of different

feeding mechanisms (Croll et al., 2018; Nerini, 1984). Given the high cost of lunge-feeding

(Potvin et al., 2012), it is likely that the different mass relationships and overall morphology of

these species reflect the combination of feeding energetics and prey availability. Due to limited

sampling, weight variation remains understudied for certain stocks, such as those in the North

Atlantic for most species. This may be resolved as the methodology of photogrammetric body

mass estimates continues to advance (Christiansen et al., 2022; Russell et al., 2023). These

techniques also offer the advantage of performing longitudinal comparisons for the same

individuals.

Analyses of early growth parameters re-affirms the convergence in relative size at weaning while

birth size in odontocetes was found to be relatively greater than that of mysticetes. This is

consistent with odontocete gestation generally lasting about 50% longer (Best et al., 1984;

Kasuya, 1977; Lockyer, 1984; Olesiuk et al., 2005). As capital breeders, mysticetes accumulate

energy stores that foster considerably faster growth during lactation than the continuous reserves

of odontocetes (Irvine et al., 2017; Oftedal, 1997). Odontocetes producing proportionally larger

neonates through longer gestations may serve to compensate for the slower postnatal growth

towards weaning size. This could be an important factor to explore in future research on the

adaptational divergence in cetacean reproduction.

Without direct data from biological examinations or photogrammetric surveys, size parameters

for certain cetacean species are estimated using other species as analogs (Huang et al., 2009;

Pastene et al., 2020). In general, the L_{mean} for large cetaceans was ~4% lower than the L_∞, and the

CVs were about 4-5% in most species. *P. macrocephalus*, *M. novaeangliae*, and *B. mysticetus*

having the highest variability in adult size (6-8%) is consistent with previous research indicating

more prolonged growth after sexual maturity and very low frequencies of physically mature

individuals (Chittleborough, 1955b, 1955a; Clarke et al., 1994; Lubetkin et al., 2012). Being able

to use variation in adult size to infer the interval of adult growth and vice-versa can have

important applications in modeling the growth and size distributions of under-studied baleen

whale stocks or fossil species (Lambert et al., 2010).

5| Conclusions

Previous reviews have attempted to provide accurate descriptions for the size of some large

mysticete species (McClain et al., 2015; Wood, 1982), but were limited in either their accuracy

or species coverage. Prioritizing primary literature has revealed several instances where the

republished data was subject to typographical errors or were missing significant details addressed

by the original authors (Klumov, 1962; Scheffer, 1974; Voronin, 1948).

This review on the size of large cetaceans has compiled a large breadth of morphometric

parameters for postnatal growth, adult variation, and body mass relationships. Analyzing the

information from both the literature and the IWC catch database facilitated descriptions of the

variance and maximum credible sizes for the current species. This review will serve as an

excellent reference for future research and provide another cornerstone in advancing

morphometric analysis that emphasizes the importance of variability within species.

Data availability

562   Supplementary figures, code, and morphometric data acquired from literature and museum

563   records can be acquired upon contact with the corresponding author. All whaling data is

564   available from the International Whaling Commission upon request to this address:

565   statistics@iwc.int

567   IWC contact page: https://iwc.int/contact

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