# Revised estimates of foetal and post-natal growth in young gray whales (*Eschrichtius robustus*)

James L. Sumich[1], Sergey A. Blokhin[2] and Piotr A. Tiupeleyev[2]

*Contact e-mail: sumichj@onid.orst.edu*

ABSTRACT

Patterns of gray whale growth in body length and weight with age are evaluated using published values of foetal and post-natal body dimensions at reported ages, supplemented with previously unpublished measured lengths of 88 mid-gestation foetuses, 82 first-summer calves and 30 second-summer whales taken in the summer/autumn Chukotkan native subsistence fishery. Gompertz growth models are fitted to foetal and post-natal lengths at age, predicting mean lengths at birth in mid-January of 4.7m, 7.9m at weaning and 8.7m at one year. The late foetal diapause in growth of length is not supported by the available data. Two equations were derived for estimating body weights from the linear body dimensions of length and maximum girth. For biomass estimates, two equations based on length alone and on both girth and length are derived. A multiple least squares regression equation fit to 14 measurements of the same whale over 14 months of captive rehabilitation predicts mean body weights at birth of 1,100–1,200kg, 5,100–5,200kg at six months (weaning), and 6,700–6,800kg at one year of age.

KEYWORDS: AGE DETERMINATION; BREEDING GROUNDS; CAPTIVITY; GRAY WHALE; GROWTH; MODELLING; MORPHOMETRICS; PACIFIC OCEAN; PHOTOGRAMMETRY; REPRODUCTION; STRANDINGS; WHALING – ABORIGINAL

## INTRODUCTION

The annual migration of eastern North Pacific gray whales (*Eschrichtius robustus*) spans as much as 50° of latitude to link summer feeding areas in the Bering and Chukchi Seas with warmer breeding, calving and assembling grounds along subtropical coastlines in winter. Most adult gray whales are thought to commence fasting in late autumn as they leave their principal high latitude feeding areas to begin the southward migration, and continue to fast for several months as they draw on their stored lipid reserves to sustain them during their absence from the feeding grounds (Nerini, 1984; Rice and Wolman, 1971; Sumich, 1986b). For the portion of adult females that are pregnant, their body reserves must also support the cost of foetal growth during late gestation as well as post-natal calf growth and metabolism for the lactation period prior to their resumption of feeding or until their calves are independently foraging. Understanding the rates and magnitudes of foetal and calf growth is requisite to estimating how pregnant/lactating females apportion their stored energy reserves during that extensive winter fast.

This population of gray whales has been the subject of commercial, scientific and subsistence harvesting for over 170 years, and extensive series of standard body lengths ($L$) of all ages and reproductive states have been obtained from harvested, stranded and captive whales. Especially useful for this study are the results of investigations conducted by the US Bureau of Commercial Fisheries along the central California coast, 1959–1969 (Rice and Wolman, 1971), reports summarising data from whales taken in the ongoing summer/autumn Chukotkan native subsistence fishery since the mid-1930s (Blokhin and Tiupeleyev, 1987; Zenkovich, 1937; Zimushko and Ivashin, 1980), and the extensive 1994–1998 aerial photogrammetric study of migrating whales of Perryman and Lynn (2002).

All mysticete species have gestation periods of approximately one year (Laws, 1959), very short for such large mammals. To grow large foetuses in so short a time period, foetuses of mysticete species experience a rapid acceleration of growth in the middle stages of development. Life history investigations have relied on standard curvilinear models (especially logistic, Gompertz and von Bertalanffy growth curves; cf. Barretto and Rosas. 2006; Mattson *et al.,* 2006) to define patterns of both pre- and post-natal growth with age. Rice and Wolman (1971) presented a foetal growth curve based on mean $L$ of 22 early, 32 middle and 55 late stage foetuses that projected a mean birth $L$ of 4.9m and a mean birth date of 10 January. Zimushko and Ivashin (1980) separated Rice and Wolman's late-term foetal $L$ data into December and January monthly groups and presented a fitted-by-eye growth curve that suggested a definite slowing of foetal growth during the last two months of gestation. No textual explanation was provided. Rice (1983) later fitted a logistic growth curve to foetal length data pooled from several earlier sources (primarily Blokhin, 1982; Rice and Wolman, 1971; Zenkovich, 1937; Zimushko and Ivashin, 1980). In this paper, Rice maintained Zimushko and Ivashin's separation of late-term foetuses by month of measurement and, because mean late-term $L$ values measured during January were the same as those obtained earlier in December, presented a growth curve that included a complete cessation of foetal growth for the final month of gestation culminating in a late January mean date of parturition at 4.6m in length. Although not described in any other species of mysticete, Rice argued that this 'diapause' in late-stage foetal growth was an adaptation to conserve maternal energy reserves by reducing investment in foetal growth after the mother leaves her polar feeding grounds in late autumn.

---

[1] *Oregon State University Hatfield Marine Science Center, Newport, OR 97365, USA.*
[2] *Pacific Research Institute of Fisheries and Oceanography (TIRNO), Vladivostok, Russia.*

Several studies have utilised measurements of dead-stranded whales as additional sources of length measurements. However, age at death of stranded calves is usually unknown, and deaths of dependent calves lacking attendant mothers may be preceded by periods of starvation and little or no growth. The mean length of 39 stranded neonates listed by Rice (1983) was 4.4m (approx. 4 SE units smaller than the 4.6m mean length of his presumably younger late-term foetuses). This difference suggests that smaller or slower-growing neonates may be less likely to survive at birth, and therefore may represent a biased sample of neonate sizes. It is not known if these smaller perinatal mortalities are offspring of primagravid or otherwise small females, as has been noted for southern right whales (Best and Rüther, 1992). For these reasons, measurements of dead stranded neonates are not incorporated into the following analyses.

Patterns of post-natal growth for young gray whales or for any other mysticete species are less well known, and few studies of immediate post-natal growth patterns in other mysticete species of similar size are available for comparison. Bowhead whale calves average about 4m at birth and 8.2m at one year (Reese *et al.*, 2001). No weight values were reported. Clapham *et al.* (1999) summarised several earlier studies of humpback whales that indicate a mean birth $L$ of 4.3–4.5m and 8–10m at one year. Most available data apply to older, often sexually mature, whales whose ages are based on counts of alternating light and dark growth layers of their wax earplugs (Aguilar and Lockyer, 1987; Blokhin and Tiupeleyev, 1987; Lockyer, 1981; Rice and Wolman, 1971; Thomson *et al.*, 1999; Zimushko and Ivashin, 1980). Each pair of adjacent light and dark layers is considered a single annual growth layer group (GLG; Perrin and Myrick, 1980).

Rice and Wolman (1971) applied a von Bertalanffy growth model to lengths of older immature animals as a function of earplug GLG number, but could not confidently assign age to sexually mature animals. Without access to animals less than one year of age (excepting foetuses), Rice and Wolman (1971) estimated that gray whale calves grow to 8.0–8.5m by weaning at 6–7 months of age and 9.0–9.5m by the end of their first year, by which time they have added 2 GLGs to their earplug lamina. From similar evidence, however, Zimushko and Ivashin (1980) concluded that gray whale calves reach 7m by weaning, 8.5m by their second summer and produce only one earplug GLG each year. Using additional length values from a captive calf (Gigi II) of known age and from six photogrammetrically measured small whales foraging during summer along the Oregon coast, Sumich (1986a) concluded, as did Zimushko and Ivashin (1980), that gray whale calves grow to about 7m by weaning. Slightly later, Blokhin and Tiupeleyev (1987) concurred with Zimushko and Ivashin (1980) that a single earplug GLG is produced each year, and provided limited evidence that young gray whales grow to 9–10m by their second summer. One purpose of this paper is to resolve these discrepancies.

A more recent study (Perryman and Lynn, 2002) contributed substantial additional information concerning patterns of calf growth. During the winter months of 1994–1998, an aerial photogrammetric study of both south- and north-migrating gray whales off the California coast was conducted. In addition to several hundred adult-size animals, body lengths were obtained of 15 south-migrating neonates throughout January ($L$ = 4.6m), 112 north-migrating calves (approximately 15 weeks old; $L$ = 7.1m), as well as of five southbound and six northbound presumed yearlings ($L$ = 8.5m). The lengths of these yearlings agree with the findings of Blokhin and Tiupeleyev (1987) if gray whales produce only one earplug GLG per year. Two gray whale calves maintained in captivity (Gigi II in 1971–72 and JJ in 1997–98) were repeatedly weighed and measured at known ages prior to their release at 13–14 months of age (Sumich *et al.*, 2001; Wahrenbrock *et al.*, 1974).

Body weights of whales typically are estimated from equations incorporating readily measured linear body dimensions (especially length) rather than from direct weighing (Ash, 1952; Laws, 1959; Lockyer, 1976; Omura, 1950; Víkingsson *et al.*, 1988). Such equations have been used to estimate weights of marine mammals as diverse as baleen whales (Laws, 1959; Lockyer and Waters, 1986; Víkingsson *et al.*, 1988), spinner dolphins (Perrin *et al.*, 2005), crabeater seals (Laws *et al.*, 2003) and Amazonian manatees (Amaral *et al.*, 2010).

Predicted weight values can accommodate seasonal and growth-related variations in body fatness if maximum girth ($G$) is included as a second independent variable. Using determinations for two parturient and five non-parturient gray whales, Rice and Wolman (1971) derived an equation to estimate body volume and define the relationship between body weight ($W$, kg), maximum girth ($G$, m) and length ($L$, m) to accommodate seasonal changes in girth.

$$W = 38G^2L \tag{1}$$

From a re-analysis of their data, supplemented with measurements of additional stranded whales and a young captive whale (Gigi II), Sumich (1986a) derived an alternative form of this equation which reversed the relative influence of girth and length on calculations of weight and provided a better statistical fit to body weight values available at that time while still maintaining integer exponents:

$$W = 18.7GL^2 \tag{2}$$

The weight data used to derive these equations were not adjusted for fluid losses during processing. Additional unmeasured variability in girth of stranded or fishery-killed whales may be caused by port-mortem abdominal distension from gases of decomposition and by the common procedure of measuring one-half G on the exposed side of fishery-harvested or large stranded whales, then doubling that value. Sumich *et al.* (2001) analysed 12 sets of weight, length and whole girth measurements of a single live whale, JJ, over the course of her 14-month captive rehabilitation (Eqn 3). The inherent complications of post-mortem distension (that increase girth) and uncompensated fluid losses during processing (that reduce weight) of most of the whales used to derive Eqn 2 may at least partially explain the 14% difference in the magnitude of the coefficients of Eqns 2 and 3.

$$W = 21.4GL^2 \tag{3}$$

The purpose of this paper is to describe the pattern of growth in length and body weight in young gray whales from early foetus stage to their second summer by re-analysing published growth data supplemented with new data from 88 mid-term foetuses, 82 post-weaning calves and 30 second-summer whales harvested under IWC quotas in the Chukotkan native subsistence fishery since 1980. Most of the data were collected prior to the unusual mortality event and consequent population contraction of 1999–2000 associated with the intense 1997–98 ENSO/El Niño event (Le Beouf *et al.*, 2000; Moore *et al.*, 2001) and all but the Rice and Wolman and Gigi II samples were obtained after the late 1970s North Pacific Ocean 'regime shift' resulting in a 1–2 week delay in the timing of the gray whale southward migration and a marked increase in the number of south-bound neonates observed in California coastal waters (Shelden *et al.*, 2004).

## METHODS

Excepting the JJ measurements, the data used in this paper were not collected specifically for the purpose of establishing growth patterns, and therefore may not necessarily be representative of the sampled populations. Because the growth rates of the two captive-raised whales differ substantially from each other and probably from non-captive whales (Sumich *et al.*, 2001), their morphometrics are used in this study only for establishing the relationship between weight, girth and length, but not for evaluating age: length relationships. Potential uncorrected biases in the data may arise from:

(1) restriction of subsistence hunts to late summer/early fall, leaving the rest of the year unsampled;

(2) failure to detect very small foetuses in adult females killed in those hunts prior to 1992;

(3) stranded animals over-representing individuals with health or nutritional conditions that may affect their rates of growth;

(4) inaccuracies of the various devices used to for obtaining body weights;

(5) possible effects of towing on gray whale carcasses, as has been reported for bowhead whales (George, 2009);

(6) post-mortem changes in body morphometrics, especially body girth; and

(7) possible changes in growth rates over the past several decades in response to increasing population size.

Some of these potential biases are discussed in the appropriate following sections. All length and girth values are reported in metres, and weight values in kilograms.

### Assignment of age

Rice and Wolman (1971) placed the mean date of conception in early December, as all the south-migrating adult females not carrying late-term foetuses that they examined in late December and January had developing corpora lutea and were assumed to be pregnant, although no early embryos were detected. Their estimated mean birth date of 10 January was later moved to 27 January (Rice, 1983) based on Rice's interpretation of a foetal diapause. The median date for parturient females migrating south past central California in the 1960s was 30 December (Rice and Wolman, 1971), presumably about two weeks prior to winter lagoon parturition. Perryman and Lynn (2002) estimated a median birth date of 13 January for southbound parturient females passing southern California. Shelden *et al.* (2004) also found that, since 1980, substantially more calves are born in the southbound migratory corridor, and the median birth dates of these neonates have clustered around mid-January. Taken together, all three studies support a mid-January mean birth date.

Post-natal ages were assigned based on the date of measurement and:

(1) for northbound calves: small body size in the close proximity to an adult-sized animal (Perryman and Lynn, 2002);

(2) for independent first-summer calves: small diameters of epizootic barnacles and the absence of larger scars of previously detached barnacles (see Bradford *et al.*, 2011 for examples);

(3) for migrating yearlings: 8–9m distribution of $L$ separate from adult $L$ (Perryman and Lynn, 2002); and

(4) for second-summer whales: earplug GLG counts.

### Growth in length

Measured standard length values obtained at estimated ages are presented and are used to derive both foetal and postnatal growth curves. The data sources, timing and locations are summarised in Table 1. Gompertz growth models were fitted to the age:length data using CurveExpert Pro, and the model with the best statistical fit was selected. Descriptive and comparative statistics were calculated with Statplus.

### Growth in weight

For the limited number of weighed whales whose length had also been measured, an empirical relationship between weight and length is derived. Weight values of whales weighed in pieces (noted in Table 4) are corrected upward by 6% to adjust for body fluids lost during flensing or necropsy, a 'baleen whale' correction factor applied by Lockyer (1976) for fin whales and by Horwood (1987) for Antarctic minke whales. The data used to derive Eqns 2 and 3 are re-analysed with measurements from two additional whales taken in the subsistence fishery and repeated

Table 1

Timing, developmental stage, migratory location, and principal sources of data used in this study. N = north; S = south.

| Mean date/date range | Growth stage | *n* | Location and data source |
|---|---|---|---|
| Feb.–Mar. 1966–69 | Early gestation | 22 | Central CA, N bound[a] |
| Jul.–Nov. 1980–91 | Mid-gestation | 88 | Chukchi Sea, foraging[b] |
| Dec.–Jan. 1966–69 | Late gestation | 55 | Central CA, S bound[a] |
| Jan. 1994–98 | Neonatal | 15 | Central CA, S bound[c] |
| 1 May 1994–98 | Mid-lactation | 112 | Central CA, N bound[c] |
| Jul.–Oct. 1987–2010 | Post-weaning | 82 | Bering/Arctic, foraging[b] |
| Jan. 1994–98 | Yearling | 11 | Central CA, S/N bound[c] |
| Jul.–Oct. 1982–2010 | 2nd summer | 30 | Chukchi Sea, foraging[b] |

Sources: [a]Rice and Wolman (1971); [b]this paper; [c]Perryman and Lynn (2002).

weighings and measures of Gigi II and JJ to derive non-linear least squares regressions describing weight as a function of length and girth. Descriptive and comparative statistics were obtained with Statplus, and mean values are listed ± 2 SE unless otherwise stated.

## RESULTS

### Foetal growth in length

Body lengths of 22 early- and 55 late-term foetuses (Rice, 1983; Rice and Wolman, 1971; D.W. Rice, pers. comm.) are combined with a previously unpublished set of 88 mid-gestation foetal length values obtained during the summer/fall Chukotkan native subsistence fishery, 1980–1991 and with 15 live neonate length values (Perryman and Lynn, 2002) to span most of the assumed 13–14 month gestation. A Gompertz growth curve (Eqn 4 and Fig. 1) provided the best statistical fit to the age:length data, with some uncertainty about the origin, reflecting the absence of very small embryos and our consequent uncertainty about the mean date of conception (Rice and Wolman, 1971).

$$L_t = 6.03e^{-e^{(2.64-0.075\bullet t)}};\ \text{t in weeks after 1 January; } r^2 = 0.95 \qquad (4)$$

The curve defined by Eqn 4 is compared in Fig. 1 to that presented by Rice (1983). The growth curve defined by Eqn 4 suggests a slight slowing of linear growth toward the end of gestation, resulting in a mid-January mean birth *L* of 4.7 ± 0.1m, rather than the complete cessation of late foetal growth and a late January mean birth date as proposed by Rice (1983).

### Post-natal growth in length

Following birth, lengths of gray whale calves of reasonably well-known ages include 112 photogrammetrically measured calves approximately 15 weeks old accompanying their mothers on their first spring northward migration (Perryman and Lynn, 2002), weanlings harvested during their first summer that were independently foraging (*segoluks* in Russian), animals from the smallest non-calf peak in the length frequency distribution of the Perryman and Lynn (2002) sample that were considered to be yearlings, and second summer whales harvested in the Chukotkan native subsistence fishery. Individual values of Perryman and Lynn's 15 week old and yearling animals were derived from their length histograms (their figs 4, 9 and 10a) that lacked dates for individual measurements. In Fig. 2, another Gompertz growth curve describes the pattern of length increase with age from birth through the second summer (~90 weeks of age). No direct measures of length at weaning age are available for non-captive gray whales. Eqn 5 predicts a mean length at weaning (26 weeks) of 7.9 ± 0.09m, with the rate of growth slowing after weaning to a mean length of about 8.7m by one year of age and to about 9m by a calf's second summer.

$$L_t = 8.85e^{-e^{(-0.47-0.068\bullet t)}};\ \text{t = estimated age in weeks following birth; } r^2 = 0.911 \qquad (5)$$

Describing juvenile growth patterns after a whale's second summer is problematic, as age determination relies solely on the difficult process of counting earplug GLGs. The whales of the Rice and Wolman sample with 2 GLGs are larger than mean *L* of the purported yearlings of the Perryman and Lynn (2002) study ($L$ = 9.2m v. 8.5m, $t_{calc}$ = 4.298, p = 0.000), supporting the interpretation by Blokhin and Tiupeleyev (1987) and by Perryman and Lynn (2002) that individuals with two earplug GLGs are in fact two years old. Accepting that only one earplug GLG is produced each year, mean length values of whales with 2, 2.5, and 3 earplug GLGs are listed in Table 2. Although the means listed in Table 2 are based on small sample sizes, they indicate a gradual increase in length to about 10–10.5m by three years of age.

Rice and Wolman (1971) reported a slight difference in length between females and males at both sexual and physical maturity. No evidence of this sexual dimorphism is apparent through second-summer whales, the oldest age for

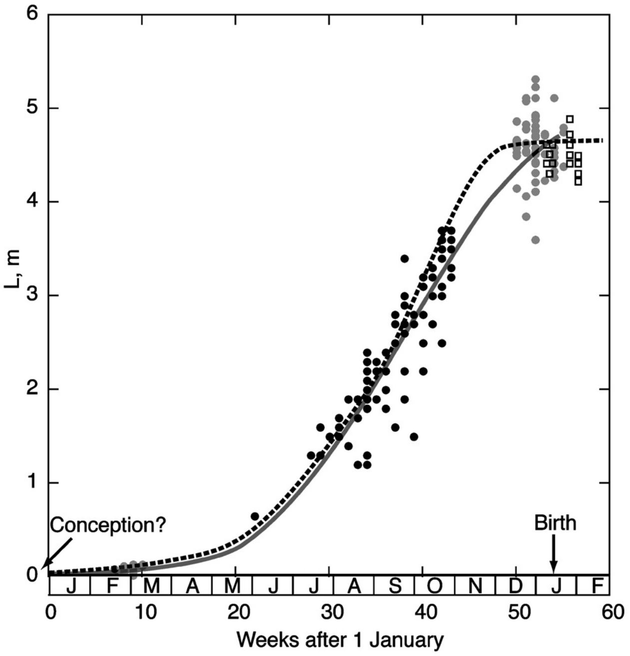

Fig. 1. Foetal and neonate *L* values and derived Gompertz growth curve (solid line and Eqn. 4). Rice's (1983) growth curve (dashed line) is superimposed on the Gompertz growth curve for comparison. Data from Rice (1983) and D. Rice (pers. comm.) in grey, the Chukotkan native subsistence fishery in black and Perryman and Lynn (2002) as open squares.

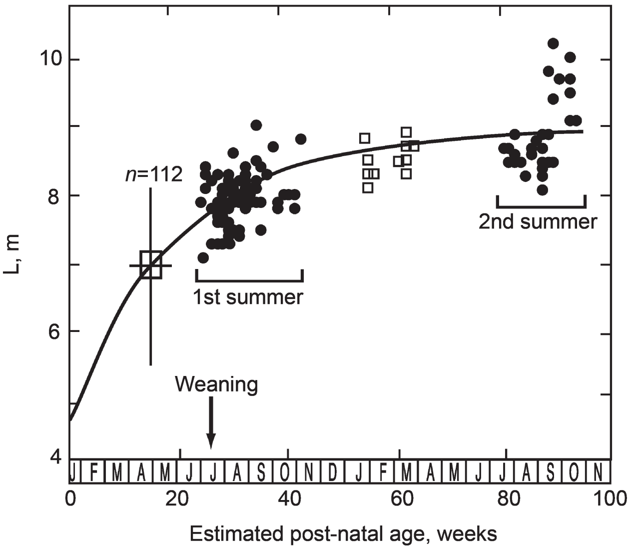

Fig. 2. Gompertz growth curve (Eqn. 5) for postnatal *L* values at estimated age. Squares and box plots (± 2SE and ranges) from Perryman and Lynn (2002); black circles, Chukotkan native subsistence fishery.

Table 2

Body lengths of young gray whales at two-three years of age.

| Attributed mean age | No. GLGs | *n* | $\bar{x}$ *L*± 2SE, *m* | Location and data source |
|---|---|---|---|---|
| 2 years | 2 | 8 | 9.2± 0.35 | California[a] |
| 2.7 years | 2.5 | 7 | 10.4± 0.28 | Arctic[b] |
| 3 years | 3 | 5 | 9.9± 0.30 | California[a] |

Sources: [a]Rice and Wolman (1971); [b]Blokhin and Tiupeleyev (1987) and this paper.

Table 3

Comparison of male and female body lengths at three ages. Late foetus data from Rice and Wolman (1971); 0.7 and 1.7 years from Chukotkan harvest (this study).

| Attributed mean age | $\bar{x}$ *L*, *m* males | *n* | $\bar{x}$ *L*, *m* females | *n* | ANOVA *F* and *p* value |
|---|---|---|---|---|---|
| Late foetus | 4.60 | 30 | 4.65 | 25 | 0.372, 0.544 |
| 0.7 years | 8.00 | 35 | 7.93 | 47 | 0.893, 0.348 |
| 1.7 years | 8.96 | 15 | 8.93 | 16 | 0.475, 0.496 |

which a reasonable sample size at attributed age is available (Table 3).

## Body weight estimates from length and girth

All weighed gray whales known to us whose lengths also have been measured are listed in Table 4. For most whales listed, girth was also measured. Whales were either weighed in pieces, weighed dead intact or weighed alive (Table 4, column 7). Reported weights of whales weighed in pieces were increased by 6% (Table 4, column 8) to compensate for fluid losses during processing.

For population-wide ecological modelling and energetics studies, weight is approximated as a power function of length (Eqn 6 and Fig. 3), derived from the values for whales numbers 1–17 (except number 13) listed in Table 4.

$$W = 8.72L^{3.07};\ r^2 = 0.920 \tag{6}$$

The $L$<9m portion of the Fig. 3 regression is replotted for comparison in Fig. 4 to the nearly identical regression (Eqn 7) of the live-weighed whale, JJ (ID no. 22–35, Table 4), with weight values from Eqn 7 being consistently about 7% greater than those of Eqn 6. Measurements of Gigi II (4 open circles, Fig. 4) generally follow the JJ curve despite her much lower growth rates in both length (5cm/week v. 8cm/week for JJ) and weight (90kg/week v. 133kg/week for JJ) over their respective periods of captivity.

$$W = 9.76L^{3.05};\ r^2 = 0.985 \tag{7}$$

The similarity of the two regression curves in Fig. 4, and the paucity of reliable girth values for wild whales <9m long in Fig. 4, suggest that the best available example of the allometric relationship between weight, length and girth for living gray whales is JJ (only two sets of W, L, with G are

Table 4

Measured girth (*G*), length (*L*) and weight (*W*) values for non-parturient gray whales.

| ID no. | Comment | *L*, *m* | *G*, *m* | *G*/*L* | *W*, kg | Weighed | *W* × 1.06 | Source |
|---|---|---|---|---|---|---|---|---|
| 1 | Originally listed as 28 feet | 8.53 | nd | – | 6,632 | In pieces | 7,030 | 1 |
| 2 | Early pregnant female | 12.70 | nd | – | 16,330 | In pieces | 17,310 | 2 |
| 3 | Stranded neonate | 4.93 | nd | – | 930 | In pieces | 986 | 3 |
| 4 | 1st summer harvested male | 8.50 | nd | – | 5,300 | Intact | – | 4 |
| 5 | Neonate | 4.75 | 2.15 | 0.45 | 901 | In pieces | 955 | 2 |
| 6 | Immature | 9.65 | 5.00 | 0.52 | 8,800 | In pieces | 9,328 | 2 |
| 7 | Immature | 9.90 | 4.85 | 0.49 | 8,868 | In pieces | 9,400 | 2 |
| 8 | Adult male | 11.72 | 6.00 | 0.51 | 15,672 | In pieces | 16,612 | 2 |
| 9 | Adult male | 12.40 | 5.50 | 0.44 | 16,579 | In pieces | 17,574 | 2 |
| 10 | Adult female, mid-gestation | 13.35 | 8.48 | 0.64 | 31,466 | In pieces | 33,354 | 2 |
| 11 | Adult female, late gestation | 13.55 | 8.80 | 0.65 | 33,816 | In pieces | 35,845 | 2 |
| 12 | Stranded | 7.81 | 3.64 | 0.47 | 3,950 | Intact | – | 5 |
| 13 | Stranded – apparent starvation | 8.10 | 3.66 | 0.45 | 3,500 | Intact | – | 5 |
| 14 | Stranded | 8.67 | 4.47 | 0.52 | 5,545 | Intact | – | 5 |
| 15 | 1st summer harvested male | 8.05 | 5.00 | 0.62 | 5,470 | Intact | – | 4 |
| 16 | 2nd summer harvested female | 8.90 | 4.60 | 0.52 | 5,865 | Intact | – | 4 |
| 17 | Gigi I at capture | 4.91 | nd | – | 1,590 | Live | – | 6 |
| 18 | Gigi II age = ~9 weeks | 5.57 | 3.12 | 0.56 | 1,970 | Live | – | 6 |
| 19 | Gigi II age = ~19 weeks | 6.10 | nd | – | 2,500 | Live | – | 6 |
| 20 | Gigi II age = ~43 weeks | 7.20 | 3.62 | 0.50 | 3,450 | Live | – | 6 |
| 21 | Gigi II age = ~58 weeks | 8.20 | nd | – | 6,380 | Live | – | 6 |
| 22 | JJ-age = 3 weeks | 4.47 | 2.22 | 0.50 | 982 | Live | – | 7 |
| 23 | JJ-age = 5 weeks | 4.72 | 2.24 | 0.47 | 1,168 | Live | – | 7 |
| 24 | JJ-age = 7 weeks | 4.93 | 2.36 | 0.48 | 1,297 | Live | – | 7 |
| 25 | JJ-age = 9 weeks | 5.13 | 2.49 | 0.49 | 1,465 | Live | – | 7 |
| 26 | JJ-age = 11 weeks | 5.46 | 2.72 | 0.50 | 1,660 | Live | – | 7 |
| 27 | JJ-age = 13 weeks | 5.68 | nd | – | 1,924 | Live | – | 7 |
| 28 | JJ-age = 15 weeks | 5.94 | 3.04 | 0.51 | 2,187 | Live | – | 7 |
| 29 | JJ-age = 17 weeks | 6.16 | nd | – | 2,523 | Live | – | 7 |
| 30 | JJ-age = 19 weeks | 6.38 | 3.33 | 0.52 | 2,860 | Live | – | 7 |
| 31 | JJ-age = 23 weeks | 6.86 | 3.66 | 0.53 | 3,534 | Live | – | 7 |
| 32 | JJ-age = 28 weeks | 7.32 | 3.73 | 0.51 | 4,355 | Live | – | 7 |
| 33 | JJ-age = 35 weeks | 7.95 | 3.81 | 0.48 | 4,799 | Live | – | 7 |
| 34 | JJ-age = 44 weeks | 8.38 | 4.65 | 0.55 | 6,781 | Live | – | 7 |
| 35 | JJ-age = 63 weeks | 9.43 | 4.90 | 0.52 | 8,889 | Live | – | 7 |

Sources: [1]Gilmore (1961); [2]Rice and Wolman (1971); [3]White and Griese (1978); [4]This study; [5]Sumich (1986a); [6]Wahrenbrock *et al.* (1974); [7]Sumich *et al.* (2001).

available for Gigi II). Using 12 sets of weight, length and whole girth measures from 3 to 63 weeks of age (ID no. 22–35 of Table 4), JJ's Eqn 3 is recalculated with non-integer exponents as Eqn 8 for a slightly improved fit ($r^2 = 0.985$ for Eqn 3).

$$W = 28.5G^{1.17}L^{1.73};\ r^2 = 0.997 \qquad (8)$$

Body weights predicted by Eqns 6, 7 and 8 were then calculated for all the whales listed in Table 4 having both girth and length measures (excepting number 13 and all JJ values) and compared to their reported or corrected weight values with paired 2-tailed t-tests. Both equations derived from JJ (Eqn 7 and 8) resulted in less deviation (Eqn 8: $t = 0.204$, $p = 0.842$; Eqn 7: $t = 0.275$, $p = 0.788$) than did Eqn 6 ($t = 0.932$, $p = 0.370$) derived from the non-JJ whales listed.

Other than JJ, few girth measurements are available for non-stranded gray whale calves older than neonates. $G/L$ measurements of five live neonates ($G/L = 0.50$; Norris and Gentry, 1974; G. Kooyman, pers. comm.) are very close to the mean found for 55 near-term foetuses (0.49 ± 0.01; Rice and Wolman, 1971). This is also similar to the mean $G/L$ of lean northbound lactating females with calves (Perryman and Lynn, 2002, converting their maximum body width measures to girth by multiplying by $\pi$) and may approximate a minimum $G/L$ for healthy lean gray whales. It is expected that calves will fatten somewhat at least until independence, however no measures of girth for live wild calves or yearlings are available. If $G/L$ remains at 0.50, Eqn 8 predicts mean weights of 1,100–1,200kg at birth, 5,100–5,200kg at six months (weaning), and 6,700–6,800kg at one year of age. An increase in $G/L$ to 0.55 (the maximum expressed by JJ) increases these predicted mean weight values by about 12%. In Table 5, weights predicted by Eqn 8 are compared to those of Eqns 6 and 7 for neonates, weanlings and yearlings.

## DISCUSSION

The previously unpublished foetal and postnatal length data presented in this paper fill critical gaps in the range of $L$ values available in the published literature to understand patterns of growth in young gray whales. The mid-gestation and first-year length data presented here bracket length at birth and provide better definition of that value. These data support the interpretation that a late-foetal growth diapause as proposed by Rice (1983) is not necessary to explain the observed distribution of neonatal length values. No similar diapause has been reported for any other mysticete species (Laws, 1959; Reese *et al.*, 2001). Rice's argument for a diapause was based on the somewhat arbitrary separation of late-term foetuses obtained in December from those of January, resulting in similar mean length values for foetuses obtained in December and in January. Using measurements of stranded winter lagoon 'neonates', Rice extended the flattened diapause curve well into February. When grouped by week rather than by month, the median date of parturient females migrating south past central California in the 1960s was 1 January, about two weeks prior to the assumed mean birth date here. Although spread over a five week interval, all 55 late-term foetuses were collected at the same stage of their mothers' southern migrations and arguably at the same stage of pregnancy and foetal development. Rice's explanation that a pre-natal diapause would conserve maternal energy reserves during her winter fast counter-intuitively requires an abrupt transition from a pre-birth condition of little or no growth to the steepest portion of the post-natal growth curve immediately following birth. Regardless of whether that growth occurs just prior to, or immediately following, birth, the fasting mother must support the entire cost of that growth

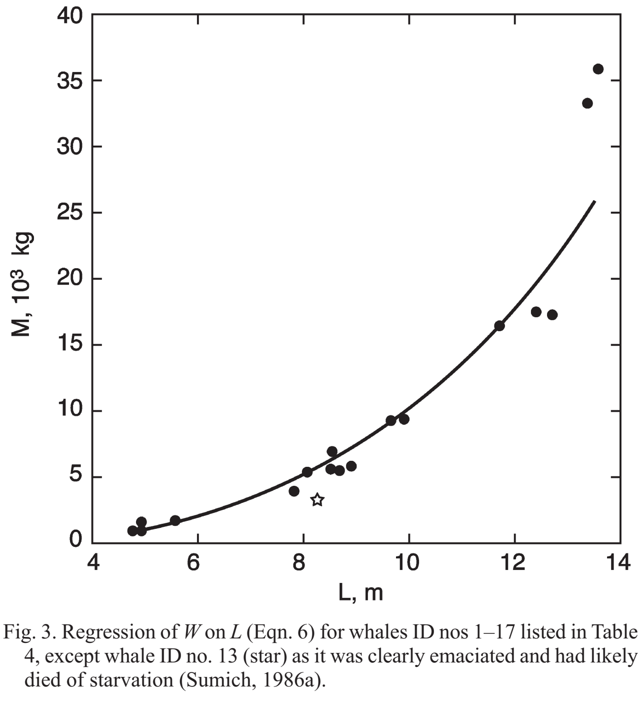

Fig. 3. Regression of $W$ on $L$ (Eqn. 6) for whales ID nos 1–17 listed in Table 4, except whale ID no. 13 (star) as it was clearly emaciated and had likely died of starvation (Sumich, 1986a).

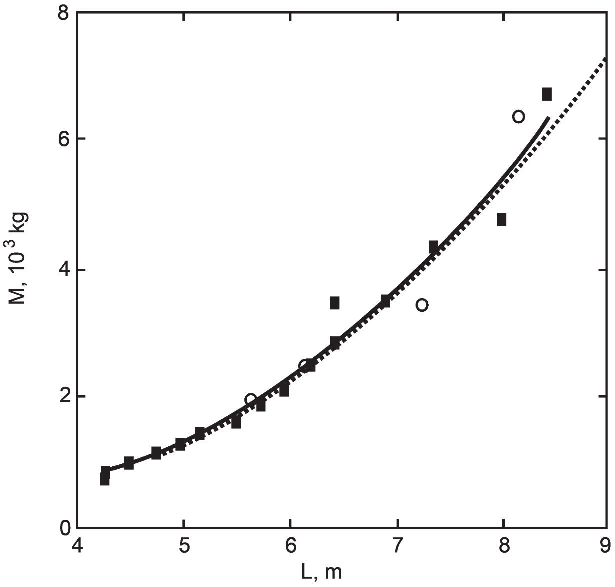

Fig. 4. Power regression of $W$ on $L$ (Eqn. 7) for JJ (black squares and solid line) compared to that of Eqn. 6 and Fig. 3 (dashed line). Open circles = Gigi II.

Table 5

Comparison of Equations 6, 7 and 8 for predicting mean $W$.

| Age | $L$, m | $W$, kg Eqn. 6 | $W$, kg Eqn. 7 | $W$, kg, Eqn. 8 G/L = 0.50 | $W$, kg, Eqn. 8 G/L = 0.55 |
|---|---|---|---|---|---|
| Neonate | 4.7 | 1,010 | 1,100 | 1,130 | 1,260 |
| 6 months | 7.9 | 4,970 | 5,340 | 5,080 | 5,680 |
| 1 year | 8.7 | 6,680 | 7,160 | 6,720 | 7,510 |

from her own tissue and energy reserves prior to regaining productive high-latitude summer foraging grounds.

A mean birth date of mid-January '…depends on the untested assumption that the probability of a near-term female giving birth is more related to the duration of her pregnancy than to her location' (Perryman and Lynn, 2002). The observed delay in the timing of the southern migration since about 1980 (Rugh *et al.*, 2001) appears to affect where a parturient female gives birth, not necessarily when she does, as indicated by the dramatic increase in the number of neonates observed in the migratory corridor rather than in winter lagoons since 1980 (Shelden *et al.*, 2004). If most conceptions do occur during the southern migration rather than in lower latitude winter 'breeding' lagoons, as proposed by Rice and Wolman (1971), a mid-January mean birth date makes the mean duration of gestation about 13.5 months.

Calculating body weights from linear body dimensions is useful to convert numerous or average values of length to mean estimates of weights and to calculations of population biomass (e.g. Vikingsson *et al.*, 1988). Both Eqns 6 and 7 contain coefficients satisfyingly close to the expected cubic function of length, with Eqn. 7 providing a better fit to available weight:length data. Both coefficients are slightly higher than that reported for North Atlantic fin whales (2.87; Vikingsson *et al.*, 1988), reflecting the more robust body shape of gray whales.

Several factors suggest JJ as a better representation of the morphometric relationship between weight, length and girth (but not of age:length relationships) than are the stranded and landed whales listed in Table 4 for typical non-pregnant gray whales. JJ's measured growth extended over most of her first 14 months, most of the age of interest of this paper.

Avoided were potential errors in:

(1) girth from doubling half-girth measures and from post-mortem distention;

(2) measured weight from unmeasured fluid losses from piecemeal weighing;

(3) JJ's G/L values are within the range expressed by most of the other non-pregnant whales in Table 4 and by the measured but unweighed non-parturient whales reported by Rice and Wolman (1971); and

(4) Both Eqns 7 and 8, derived from JJ's measurements, better predict the measured weights of the other whales listed in Table 4 than does Eqn 6 that was derived from the measurements of those whales.

For these reasons, Eqn 8 is considered a better predictor of body weight when both length and girth are known, and Eqn 7 when only length is measured or when measured girth is suspected of post-mortem distortion.

The substantial deviation of the weight values of the two larger and much fatter pregnant females (ID nos 10 and 11) from the regression of Fig. 4 reflects their wider bodies and different body shapes (Perryman and Lynn, 2002). These large females exemplify the problem of estimating weight from length alone without compensating for changes in G/L or other morphometrics due to growth, seasonal fattening or pregnancy. For whales that are neither late pregnant nor in the early stages of lactation, these changes are better accommodated when girth is included as a second independent variable. Although derived for young gray whales, Eqn 8 should apply equally well to adult whales with G/L ratios of 0.50–0.55.

The predicted mean weight at weaning (5,100–5,200kg) for wild calves conforms reasonably well to the assumption of Lee *et al.* (1991) that, for eutherian mammals, weight at weaning is isometrically related to birth weight as: weaning weight = 4 × (birth weight). However, any estimate of weight at weaning is necessarily sensitive to the selection of G/L of wild calves.

Eqn 8, incorporating girth as well as length, accommodates differences between lean and fat body conditions, with $L$ having a greater effect on W than girth. Lockyer and Waters (1986) also found that $L$ was more influential than girth on W of southern hemisphere fin and sei whales. Vikingsson *et al*. (1988) presented similar results for fin whales but not for sei whales in the North Atlantic, and attributed the discrepancy to possible differences in body proportions of these two populations.

The results of this study suggest that the effect of girth measurements of stranded animals on calculated body weights are quite variable and, because of post-mortem distortion, reduce their usefulness as bases for calculating body weight. Perryman and Lynn (2002) have demonstrated that aerial photogrammetry can be an effective technique to obtain accurate body length and maximum width (a proxy for girth) measurements of gray whales to evaluate overall individual nutritive condition. We encourage continued periodic use of this technique over decadal time periods to better define sizes and body conditions of calves at weaning and to detect possible changes in growth rates and body sizes as a consequence of this population having reached (or even surpassed) its carrying capacity (Moore *et al.*, 2001).

## ACKNOWLEDGMENTS

We thank the Animal Care Department staff at SeaWorld, San Diego, for access to measurement data of JJ, and Drs D. Rice and A. Wolman for access to original unpublished data of their gray whale study. Drs Eric Wahrenbrock and Gerald Kooyman also provided access to their unpublished data. Christina Lockyer (Age Dynamics), Jeff Jacobsen (Humboldt State University), Susan Chivers and Wayne Perryman (NOAA, Southwest Fisheries Center) and two anonymous reviewers provided valuable suggestions and criticisms on earlier versions of the manuscript.

### REFERENCES

Aguilar, A. and Lockyer, C.H. 1987. Growth, physical maturity and mortality of fin whales *Balaenoptera physalus* inhabiting the temperate waters of the northeast Atlantic. *Can. J. Zool.* 65(2): 253–64.

Amaral, R.S., da Silva, V.M.F. and Rosas, F.C.W. 2010. Body weight/length relationship and mass estimation using morphometric measurements in Amazonian manatees *Trichechus inunguis* (Mammalia: Sirenia). *Mar. Bio. Rec.* 3: 1–4.

Ash, C.E. 1952. The body weights of whales. *Norsk Hvalfangsttid* 41: 364–74.

Barreto, A. and Rosas, F. 2006. Comparative growth analysis of two populations of *Pontoporia blainvillei* on the Brazilian coast. *Mar. Mammal Sci.* 22: 644–53.

Best, P.B. and Rüther, H. 1992. Aerial photogrammetry of southern right whales, *Eubalaena australis*. *J. Zool.* 228: 595–614.

Blokhin, S.A. 1982. Investigations on gray whales taken off Chukotka in 1980. *Rep. int. Whal. Commn.* 32: 375–80.

Blokhin, S.A. and Tiupeleyev, P.A. 1987. Morphological study of the earplugs of gray whales and the possibility of their use in age determination. *Rep. int. Whal. Commn* 37: 341–45.

Bradford, A.L., Weller, D.W., Burdin, A.M. and Brownell Jr., R.L. 2011. Using barnacle and pigmentation characteristics to identify gray whale calves on their feeding grounds. *Mar. Mammal Sci.* 27: 644–51.

Clapham, P.J., Wetmore, S.E., Smith, T.D. and Mead, J.G. 1999. Length at birth and at independence in humpback whales. *J. Cetacean. Res. Man.* 1(2): 141–46.

George, J.C. 2009. Growth, morphology and energetics of bowhead whales (*Balaena mysticetus*). PhD dissertation, University of Alaska, Fairbanks. 168pp.

Horwood, J. 1987. *The Sei Whale: Population Biology, Ecology & Management*. Croom Helm, London, New York, Sydney. [xi]+375pp.

Laws, R.M. 1959. The foetal growth rates of whales with special reference to the fin whale, *Balaenoptera physalus* Linn. *Discovery Rep.* 29: 281–308.

Laws, R.M., Baird, A. and Bryden, M.M. 2003. Size and growth of the crabeater seal *Lobodon carcinophagus* (*Mammalia: Carnivora*). *J. Zool. (Lond.)* 259: 103–08.

Le Beouf, B., Perez-Cortes, M., Urban, R., Mate, B.R. and Ollervides, U. 2000. High gray whale mortality and low recruitment in 1999: potential causes and implications. *J. Cetacean Res. Manage.* 2: 85–99.

Lee, P.C., Majluf, P. and Gordon, I.J. 1991. Growth, weaning and maternal investment from a comparative perspective. *J. Zool.* 225: 99–114.

Lockyer, C. 1976. Body weights of some species of large whales. *J. Cons. Int. Explor. Mer* 36(3): 259–73.

Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the Southern Hemisphere. *FAO Fisheries Series No. 5 (Mammals in the Sea)* 3: 379–487.

Lockyer, C. and Waters, T. 1986. Weights and anatomical measurements of northeastern Atlantic fin (*Balaenoptera physalus*, Linnaeus) and sei (*B. borealis*, Lesson) whales. *Mar. Mammal Sci.* 2(3): 169–85.

Mattson, M., Mullin, K., Ingram, G. and Hoggard, W. 2006. Age structure and growth of the bottlenose dolphin (*Tursiops truncatus*) from strandings in the Mississippi Sound region of the north-central Gulf of Mexico from 1986 to 2003. *Mar. Mammal Sci.* 22: 654–66.

Moore, S., Urbán R, J., Perryman, W., Gulland, F., Perez-Cortes, H., Rojas-Bracho, L. and Rowles, T. 2001. Are gray whales hitting ‘K’ hard? *Mar. Mammal Sci.* 17(4): 954–58.

Nerini, M. 1984. A review of gray whale feeding ecology. pp.423–50. *In*: Jones, M.L., Swartz, S.L. and Leatherwood, S. (eds). *The Gray Whale, Eschrichtius robustus*. Academic Press, Inc., Orlando, Florida. xxiv+600pp.

Norris, K.S. and Gentry, R.L. 1974. Capture and harnessing of young California gray whales, *Eschrichtius robustus*. *Mar. Fish. Rev.* 36(4): 58–64.

Omura, H. 1950. On the body weight of sperm and sei whales located in the adjacent waters of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 4: 1–13.

Perrin, W.F., Dolar, M.L.L., Chan, C.M. and Chivers, S.J. 2005. Length–weight relationships in the spinner dolphin (*Stenella longirostris*). *Mar. Mammal Sci.* 21(4): 765–78.

Perrin, W.F. and Myrick, A.C. 1980. *Report of the International Whaling Commission (Special Issue 3). Age Determination of Toothed Whales and Sirenians*. International Whaling Commission, Cambridge, UK. 229pp.

Perryman, W.L. and Lynn, M.S. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *J. Cetacean Res. Manage.* 4(2): 155–64.

Reese, S.C., Calvin, J.A., George, J.C. and Tarpley, R.J. 2001. Estimation of fetal growth and gestation in bowhead whales. *J. Am. Stat. Assoc.* 96(455): 915–38.

Rice, D.W. 1983. Gestation period and fetal growth of the gray whale. *Rep. int. Whal. Commn* 33: 539–44.

Rice, D.W. and Wolman, A.A. 1971. *The Life History and Ecology of the Gray Whale (Eschrichtius robustus)*. American Society of Mammalogists, Special Publication No. 3, Stillwater, Oklahoma. viii+142pp.

Rugh, D.J., Shelden, K.E.W. and Schulman-Janiger, A. 2001. Timing of the gray whale southbound migration. *J. Cetacean Res. Manage.* 3(1): 31–39.

Shelden, K.E.W., Rugh, D.J. and Schulman-Janiger, A. 2004. Gray whales born north of Mexico: indicatory of recovery or consequence of regime shift? *Ecol. Appl.* 14(6): 1789–805.

Sumich, J.L. 1986a. Growth in young gray whales (*Eschrichtius robustus*). *Mar. Mammal Sci.* 2(2): 145–52.

Sumich, J.L. 1986b. Latitudinal distribution, calf growth and metabolism, and reproductive energetics of gray whales, *Eschrichtius robustus*, PhD dissertation, Oregon State University. 216pp.

Sumich, J.L., Goff, T. and Perryman, W.L. 2001. Growth of two captive gray whale calves. *Aquat. Mamm.* 27(3): 231–33.

Thomson, R.B., Butterworth, D.S. and Kato, H. 1999. Has the age at transition of Southern Hemisphere minke whales declined over recent decades? *Mar. Mammal Sci.* 15(3): 661–82.

Víkingsson, G., Sigurjónsson, J. and Gunnlaugsson, T. 1988. On the relationship between weight, length and girth dimensions in fin and sei whales caught off Iceland. *Rep. int. Whal. Commn* 38: 323–26.

Wahrenbrock, E.A., Maruschak, G.F., Elsner, R. and Kenney, D.W. 1974. Respiration and metabolism in two baleen whale calves. *Mar. Fish. Rev.* 36(4): 3–8.

White, S.B., and Griese, H.J. 1978. Notes on lengths, weights, and mortality of gray whale calves. *J. Mammal.* 59: 440–41.

Zenkovich, B.A. 1937. Weighing of whales. *C. R. (Doklady) Acad. Sci, URSS* 16: 177–82.

Zimushko, V.V. and Ivashin, M.V. 1980. Some results of Soviet investigations and whaling of Gray whales (*Eschrichtius robustus*, Lilljeborg, 1961). *Rep. int. Whal. Commn* 30: 237–46.