



# Timing hypothesis explains the mystery of the missing blue whale calves

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**ABSTRACT:** Few mother–calf pairs are sighted in blue whale *Balaenoptera musculus* populations worldwide, averaging only 3.1% (95% CI 2.7–3.4%) of sighted individuals, despite 33 to 50% annual pregnancy rates among mature females. Multiple hypotheses were examined to explain the low rates of sighted calves. Observed rates are too low to be explained by low fetal survival, low calf survival, low birth rates, or calf separation from mothers, although mother–calf pairs might avoid higher-density regions where field studies are concentrated, and accounting for males and immature individuals reduced the expected proportion of mother–calf pairs to 7 to 12%. However, the timing hypothesis best explained observed patterns, by proposing that most blue whales produce calves shortly after departing their summer feeding grounds and wean their calves 7 mo later, on their return. A conceptual model of this hypothesis, with some variability around calving dates and a few year-round births, predicted mother–calf proportions peaking in winter at 8 to 9% and reaching a low of 1 to 4% in summer. These predictions matched the low proportions observed in 7 of 8 summer feeding regions (1.5–3.5%), but not off New Zealand (9.8%), while in winter, observed proportions were high in the Gulf of California (12.3%) and Timor Trough (9.3%) but lower in the Galapagos (3.8%). The lowest mother–calf proportion was off Sri Lanka (0.7%), where blue whales reside year-round. These results suggest that the mystery of the missing blue whale calves can largely be explained by mothers calving immediately after leaving summer feeding grounds and weaning on their return.

**KEY WORDS:** Baleen whales · Calving · Killer whales · Migration · Predation · Reproduction · Weaning

## 1. INTRODUCTION

Blue whale calving has long been shrouded in mystery, despite extensive 20<sup>th</sup> century whaling and more recent long-term sighting studies. Only 2 calving events have ever been recorded, and both are somewhat anomalous. The first occurred on 14 September 1911 in Saldanha Bay, South Africa, when a 29.0 m female blue whale was encountered by whalers just after giving birth and lying exhausted on the surface (Olsen 1914). The whalers promptly harpooned both mother and calf and noted that the mother produced 240 barrels of oil and had 20 to 30 cm blubber thickness, while the calf was 7.03 m long with curled flukes and with an attached umbilical cord. Both the location

and timing of this birth are unusual: Antarctic blue whales are usually found 65 to 100 km offshore in this area (Olsen 1914), and calving peaks in early May, not September (Mackintosh & Wheeler 1929). The second observed calving event was in Trincomalee Harbor, Sri Lanka, on 24 January 1946 (Deraniyagala 1948). The mother had stranded the previous day in shallow waters, and despite an attempt to tow her back out of the harbor, she stranded again and gave birth. After giving birth, the mother was successfully towed into deep waters, but no further mention is made of the size or status of the newborn calf. In addition to the possibility that the birth was premature due to the stress of stranding, the reported mother length (18.3 m) is short even for pygmy blue

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whales—at this length, only an estimated 25% of northern Indian Ocean blue whales are sexually mature (Branch & Mikhalev 2008). While it might seem incredible that only 2 blue whale births have ever been documented, blue whales do not aggregate in nearshore waters for calving (Ford & Reeves 2008), which would result in easier viewing, unlike some other baleen whale species. Even in baleen whale species that do aggregate in nearshore calving regions, only a small handful of births have been observed, in Atlantic right whales (Zani et al. 2008), southern right whales (Shuttleworth et al. 2024), humpback whales (e.g. Ransome et al. 2022), and gray whales (Mills & Mills 1979).

While births are rarely documented, the real mystery of the missing calves in blue whales comes from the chasm between pregnancy rates among sexually mature female blue whales and the number of calves sighted in recent decades during long-term studies. Pregnancy rates from a variety of data sources, including historical whaling, are consistent with calving every 2 to 3 yr, i.e. 33 to 50% (e.g. Mackintosh 1942, Tomilin 1967, Sears & Perrin 2009). Observed pregnancy rates among sexually mature females are 42.9% ( $n = 17910$ ) for Antarctic blue whales from Norwegian and British whaling data from 1933–1934 to 1962–1963 during December to April (Mizroch 1981), 33.4% ( $n = 51$ ) for northeast Pacific blue whales from progesterone data (Atkinson et al. 2020), 31% ( $n = 241$ ) for central and western North Pacific blue whales (Brueggeman et al. 1985), and 35.6% for pygmy blue whales from whaling data in the southern Indian Ocean in February before declining to 6.9% in April (Ichihara 1966). These pregnancy rates are far higher than would be inferred from the rare sightings of mother–calf pairs in long-term blue whale studies. For example, only 35 calves have been seen during 45 yr (<2% of sightings) in the Gulf of St. Lawrence (R. Sears pers. comm., 27 Oct 2023), and there were only 76 calf sightings out of 3660 individuals (2.1%), based on high-quality photographs taken on the US west coast (Wachten-donk et al. 2022).

To address this mystery of the missing blue whale calves, I compiled data on the proportion of calves that are sighted in different areas of the world and then examined whether these values can be explained by a variety of hypotheses. The examined hypotheses include a low proportion of mature females, *in utero* mortality, low calf survival rates, calf behavior, mother–calf avoidance of well-studied aggregation areas, and the timing of calving and weaning compared to the timing of field studies.

## 2. METHODS

### 2.1. Compilation of field studies

I obtained the proportion  $p$  of mother–calf pairs from a suite of long-term field studies on blue whales, either from published records or by contacting key involved scientists. The definition of calves used here is individuals that are small (<16 m), closely associated with females, and therefore assumed to be suckling. It should be noted that although aerial footage shows that suckling calves rarely leave the sides of their mother (Smultea et al. 2017, 2022), this is not always true when the mother is feeding (D. Gendron pers. comm., 18 Nov 2024). Studies were included if they sighted large numbers of blue whales (all sighted  $\geq 89$  individual blue whales) and were conducted over multiple field seasons or broad geographic areas. Proportions of mother–calf pairs were calculated to be directly comparable to pregnancy rates, i.e.  $p = c/(m + n)$ , where  $c$  is the number of calves,  $m$  is the number of mothers, and  $n$  is the number of all individuals who are neither mothers nor calves. Since mothers and calves are sighted as pairs,  $m = c$ , and this equation could also be written as  $p = m/(m + n)$ . For each study, the 95% CI was calculated, assuming this proportion followed a binomial distribution.

### 2.2. Hypothesis testing

Multiple hypotheses could explain the observed proportions of calves in blue whale populations. Here, following the method of multiple working hypotheses (Chamberlin 1897), a series of hypotheses are briefly outlined together with analyses that can be used to assess their validity.

H1: Low proportion of mature females in the population. Observed pregnancy rates among sexually mature females may be consistent with relatively low proportions of mother–calf pairs in sightings if most whales in a population are males or juveniles. A simple age-structured model was built to calculate the proportion of mother–calf pairs among all age 1+ males and females. There is little uncertainty about the proportion of females  $q_f = 0.479$  after birth (Branch & Monnahan 2021) or average age at sexual maturity  $t_m = 10$  yr (Ichihara 1966, Sazhinov 1970, 1980, Ohsumi 1979, Branch 2008), but other parameters are less well known and are assumed to come from a uniform range: non-calf survival  $S^{1+} \sim U[0.93, 0.99]$  (Ohsumi 1979, Branch et al. 2004, Ramp et al. 2006); calf survival  $S_j \sim U[0.545, 0.93]$  (Branch et al. 2004, Ugalde de

la Cruz 2015), and pregnancy rate  $P_r \sim U[0.33, 0.50]$  to account for calving every 2 to 3 yr. Blue whale populations are expected to be recovering after whaling (Sigurjónsson & Gunnlaugsson 1990, Best 1993, Branch et al. 2004, Monnahan et al. 2015); therefore, parameter combinations leading to population growth of less than 1% yr<sup>-1</sup> were removed. Simulations were conducted as follows until 1000 samples were saved: (1) draw a value for each parameter; (2) run the model for 1000 yr (to reach stable age distribution and stable population growth rate); (3) calculate the population growth rate in the final year at equilibrium; (4) if the population growth is greater than 1%, then save the parameter values; otherwise, repeat steps 1 to 4; and (5) calculate the proportion of mother–calf pairs at birth and at weaning, assuming that 7/12 of the mortality in the first year occurs between birth and weaning and that weaning is 7 mo after birth (e.g. Mackintosh & Wheeler 1929).

H2: *In utero* mortality. High fetal mortality could explain the low proportions of mother–calf pairs. The literature was examined for evidence of such mortality in blue whales, and a global compilation of 176 blue whale strandings with length data and confirmed species identification (T. Branch, K. Randrup & R. Brownell unpubl., 13 Sep 2024) was examined for records of very small blue whales that might be aborted fetuses.

H3: Low birth rates. Birth rates may have declined since the whaling era due to density-dependent effects, interspecific competition, or climate change. A review of the literature was conducted for evidence of blue whale populations approaching pre-whaling levels, competition, and climate change impacts on blue whales.

H4: Low calf survival. The discrepancy between pregnancy rates and the observed number of calves could be explained by very low calf survival from ship strikes, fishing gear entanglement, lack of nutrition, or killer whale predation. A literature review was conducted for estimates of calf survival in blue whales and for studies reporting observations of killer whale attacks or killer whale rake marks on their bodies.

H5: Calf behavior and visibility. If calves are less visible than mothers or spend considerable time away from mothers before weaning, this would reduce the number of calves identified in field studies. A literature review was conducted for observational studies of mother–calf pairs that could shed light on this issue.

H6: Mother–calf avoidance of aggregations. Mother–calf pairs may choose to avoid aggregations of blue whales, which is where field studies are

usually concentrated. Avoidance of aggregations would make sense if the primary driving force of calf mortality is killer whales *Orcinus orca*, since blue whales are flight species that do not rely on group defense, unlike fight species such as humpback whales *Megaptera novaeangliae* and gray whales *Eschrichtius robustus* (Ford & Reeves 2008). A review was conducted of satellite tagging and passive acoustic studies of blue whales to determine if some individuals (that could be mothers with newborn calves) avoid regions with high densities of blue whales.

H7: Timing of calving and weaning. The absence of sighted mother–calf pairs may reflect the timing of calving and weaning relative to historical whaling and recent field studies that have focused on summer feeding areas where blue whales congregate in higher densities. If blue whales give birth shortly after leaving summer feeding areas and wean their calves before returning, then summer whaling data would show high proportions of pregnant females, but mother–calf pairs would be rare in summer sightings. To examine this possibility, a literature review was conducted to determine birth size, birth timing, weaning size, and weaning timing for blue whale populations, largely based on whaling data. From the resulting dates, a conceptual model was created to illustrate the predictions of this hypothesis as outlined below.

The conceptual model of the timing hypothesis is intended as a model for seasonal patterns in calf availability, although precise estimates of all parameters are not possible to obtain. The conceptual model assumes that calving has a peak date, with some variability (represented by a normal distribution with a mean and SD), but that there is also a small constant probability of calving during the remaining months to account for year-round conceptions. Antarctic blue whales were the largest population, the most impacted by whaling, and the most intensively studied during the whaling era, and therefore parameters are generally based on this population. Extensive fetal data have been used by multiple studies to estimate dates for conception, birth, and weaning and the corresponding lengths for each. The most meticulous of these studies was Mackintosh & Wheeler (1929), and subsequent studies have confirmed their findings. They estimated birth to occur at 7 m and weaning at 16 m, and based on a plot that pieced together fetal length and calf length by day of the year (Mackintosh & Wheeler 1929, p. 435), they estimated calving to peak in early May (range early Mar–early Jul), and weaning to peak in early December (range early Sep–early Mar). Gestation was estimated to be slightly over 10 mo, and calf growth in length was estimated

to be approximately linear from birth to weaning 7 mo later (Mackintosh & Wheeler 1929, p. 442). Subsequent papers have largely estimated (or assumed) similar timing and sizes of blue whales at these stages of development (Laurie 1937, Laws 1959), but with total gestation between 10 and 11 mo (Laws 1959, Lockyer 1984). The total gestation period is difficult to pinpoint because there is a period after conception where the embryo is both free-floating and too small to detect followed by a period after implantation where detection of the embryo remains unlikely. The smallest detected embryo was 6.5 mm long (Gill 1926).

Fewer data are available for other blue whale populations. Southern Indian Ocean pygmy blue whales are likely somewhat smaller at birth, perhaps 6.0 to 6.5 m (Ichihara 1966, Sazhinov 1980), while still following the same growth timing as Antarctic blue whales (Ichihara 1966, Barlow et al. 2023), suggesting a slightly earlier calving (Apr–May) than Antarctic blue whales. Fetal data for New Zealand pygmy blue whales are only available for April and May and are consistent with an April to June peak in calving (Barlow et al. 2023). Northern Indian Ocean blue whales

are not assessed here, given an ongoing discussion about their calving season (Mikhalev 2000, Branch et al. 2019, Cerchio et al. 2020). For the Northern Hemisphere blue whale populations, fewer whaling data are available, but I assume that calving and weaning are 6 mo out of phase with the Southern Hemisphere, and therefore calving would peak in October to November and weaning in April to June.

The peak timing of calving does not account for the spread of possible conception dates, and fetal data suggest that a small proportion of blue whales are conceived throughout the year (Mackintosh & Wheeler 1929, Laws 1959). For example, in the figure on p. 435 in Mackintosh & Wheeler (1929; their Fig. 149, p. 435), about 15% of 10 to 14 m calves and 25% of 14 to 16 m calves were born outside the peak calving period. Thus, the timing hypothesis needs to make assumptions about the variation in the peak timing and the proportion of calves born outside the usual calving period.

Therefore, the conceptual model (Fig. 1) assumes a normal distribution for calving around 1 May (Day 121), with an SD of 39 d, and a background minimum calving rate such that 10% of all calves are born in the

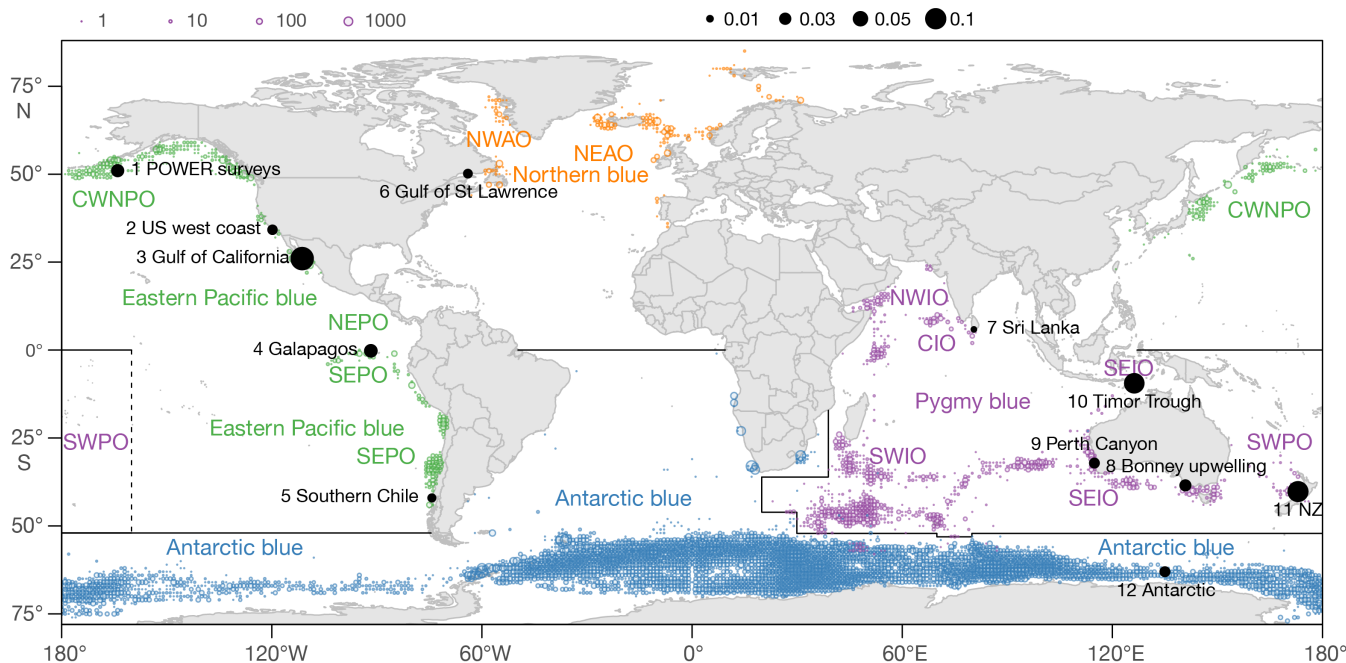


Fig. 1. Regions with data, with the size of the solid black circles related to the proportion of mother–calf pairs. Winter data are available only for the Gulf of California, Galapagos, and Timor Trough. Sri Lanka is not classified by season, and other sites are summer sites. Open circles depict historical catches colored by subspecies (Antarctic, pygmy, eastern Pacific, and northern blue whales). Acronyms represent individual blue whale populations, and numbered labels represent the study areas referred to in the text. POWER: Pacific Ocean Whale and Ecosystem Research; NWA0: northwest Atlantic Ocean; NEAO: northeast Atlantic Ocean; CWNPO: central and western North Pacific Ocean; NEPO: northeast Pacific Ocean; NWIO: northwest Indian Ocean; CIO: central Indian Ocean; SEPO: southeast Pacific Ocean; SWIO: southwest Indian Ocean; SWPO: southwest Pacific Ocean; SEIO: southeast Indian Ocean; NZ: New Zealand. Source of catch data: Allison (2024)

off-season of August to January (all dates for the Southern Hemisphere). Weaning is assumed to occur 7 mo (213 d) after birth. Calf survival is assumed to be  $0.7 \text{ yr}^{-1}$ , with mortality spread evenly across all days of the year. The annual birth rate is assumed to be 0.429 per sexually mature female. This provides predictions of the proportion of mature females accompanied by calves on each day of the year. To estimate the proportion of mother–calf pairs among all sightings, these were multiplied by the proportion of mature females in the population using the age-structured model outlined in hypothesis H1 but parameterized with the mean values outlined above: age at maturity  $t_m = 10 \text{ yr}$ , survival of non-calves  $S^{1+} = 0.96$ , calf survival  $S_j = 0.7 \text{ yr}^{-1}$ , proportion of females  $q_f = 0.479$ , and pregnancy rate  $P_r = 0.429$ .

### 3. RESULTS

#### 3.1. Compilation of field studies

Mother–calf proportions were obtained from 14 blue whale studies in 12 regions covering 8 blue whale populations (Table 1, Fig. 1). Nine of the 14 long-term studies focused on summer feeding areas where blue whales are most concentrated and included 87% of total sightings and 65% of mother–calf sightings. The 5 studies in winter regions were conducted in the Gulf of California, a calving and feeding region (Gendron 2002, Sears et al. 2013); Timor Trough, a migration corridor and feeding area (Burton et al. 2023); the Galapagos, a feeding area for Southeast Pacific blue whales and possibly also northeast Pacific blue whales (Denkinger et al. 2023); and off southern Sri Lanka, where blue whales are present year-round (Priyadarshana et al. 2016). Across all studies, 11 469 individual blue whales were sighted, including 339 mother–calf pairs, for an overall proportion of 3.1% mother–calf pairs (95% CI 2.7–3.4%). In total, 5 of the 14 studies reported more than 4% mother–calf pairs: 11% in the Gulf of California in February to March (Sears et al. 2013); 15.7% in the Gulf of California in January to May (Gendron 2002); 7.9% in the Gulf of Corcovado and outer coast of Chile in January to April (Hucke-Gaete et al. 2004, 2005); 9.3% in the Timor Trough south of Timor Leste in July to September (Burton et al. 2023); and 9.8% in the South Taranaki Bight, New Zealand, in January to February (Barlow et al. 2018, D. Barlow & L. Torres pers. comm.). For analysis by regions, I combined the 2 studies from the Gulf of California (Gendron

2002, Sears et al. 2013) to obtain 104 sightings of mother–calf pairs out of 950 sightings (overall proportion 12.3%, 95% CI 10.2–14.6%), and I combined the 2 studies in the region of Chiloe Island, Chile (Hucke-Gaete et al. 2004, 2005, Galletti Vernazzani et al. 2012), for 20 mother–calf pairs out of 1372 sightings (overall proportion 1.5%, 95% CI 0.9–2.2%).

#### 3.2. Hypothesis testing

H1: Low proportion of mature females in the population. Simulations with the assumed range of parameter values produced median equilibrium population growth rates of 3.6% (95% CI 1.6–6.8%), mother–calf proportion at birth of 9.9% (95% CI 8.3–11.8%), and mother–calf proportion at weaning of 8.0% (95% CI 6.9–8.9%). The least known of the input parameters is calf survival, which was assumed to be drawn from a uniform distribution between 0.545 and 0.93. If calf survival is instead fixed at the lower bound of 0.545, then many parameter draws (31% of the total) result in population growth rates less than 1% and are discarded, retaining mainly draws with higher adult survival, resulting in paradoxically higher mother–calf proportions at birth of 11.4% (9.7–12.5%) and at weaning of 8.3% (7.1–9.2%). If calf survival is fixed at the upper bound of 0.93, the opposite effect is observed, where only 2% of draws are discarded, more draws are retained with lower adult survival, and the mother–calf proportion at birth is 9.0% (8.0–9.9%) and at weaning is 8.6% (7.6–9.5%). Overall, mother–calf proportions in sightings are expected to be in the range of 7 to 12%.

H2: *In utero* mortality. Only 1 paper (Ichihara 1962) was found that examined the occurrence of dead fetuses *in utero* in baleen whales, based on whaling data. Most of the dead fetuses were fin whales (17 of 20), with 2 reported for blue whales. In fin whales, they comprised 0.14% of all fetuses. Mortality *in utero* was more common at fetal length extremes and in multiple pregnancies (Ichihara 1962). Stranding data revealed only 1 small individual that could have been a failed pregnancy—a 6.35 m female with all-black baleen that stranded live on 20 December 1976 near Ovari, Gulf of Mannar, India (Marichamy et al. 1984). A reported 7.42 m stranding in South Australia (Waite 1926) was not a blue whale, given skull features and baleen color, and 3 additional strandings between 6.0 and 6.5 m (Baby 1996, Tiwari & Varu 2001, Khalaf 2015) do not include enough information to be cer-

Table 1. Proportion of mother–calf pairs sighted in different regions of the world. The 95% CIs are obtained by assuming they come from a binomial distribution. Region numbers are those plotted in Figs. 1 & 2. IWC-POWER: International Whaling Commission's Pacific Ocean Whale and Ecosystem Research; JARPA: Japanese Whale Research Program under Special Permit in the Antarctic

Population	Study region	Main activity in region	Peak months	No. of sightings (all individuals)	Mother–calf pairs No.	Proportion	95% CI	Notes	Source
Central and western N Pacific	1. North Pacific	Summer feeding	Aug–Sep	89	3	0.035	0.006–0.081	IWC-POWER surveys from 2010 to 2022, primary search effort only (52788 km); including off effort, 111 individuals and 4 calves	Annual cruise reports, e.g. Murase (2022), Katsumata & Matsuoka (2023)
NE Pacific	2. US west coast	Summer feeding	June–Oct	3660	76	0.021	0.017–0.026	Based on individuals with good photo-ID for body condition	Wachtendonk et al. (2022)
NE Pacific	3. Gulf of California	Winter feeding	Feb–Mar	~700	70	0.11	0.088–0.137	Number of individuals with photo-ID	Sears et al. (2013)
NE Pacific	3. Gulf of California	Winter feeding	Jan–May	250	34	0.157	0.112–0.208	Number of individuals with photo-ID	Gendron (2002)
SE Pacific	4. Galapagos	Winter feeding	June–Sep	164	6	0.038	0.013–0.072	From 2001 to 2018, 6 calves observed from 65 sightings with more than 164 individuals, all calves sighted Jun–Sep, possible that some calves not reported	Denkinger et al. (2023), J. Denkinger (pers. comm., 1 Dec 2023)
SE Pacific	5. Chile, outer coast 40–44° S	Summer feeding	Feb–Apr	1140	3	0.002	0.000–0.006	From 2004 to 2010, aerial and boat surveys, 1 mother sighted with, without, and with a calf during 18 d in Feb; photo-ID catalogue contained 363 individuals	Galletti Vernazzani et al. (2012)
SE Pacific	5. Chile, outer coast and Gulf of Corcovado	Summer feeding	Jan–Apr	232	17	0.079	0.046–0.118	Data from land, aerial, and boat surveys in 2003–2005	Hucke-Gaete et al. (2004), Hucke-Gaete et al. (2005)
NW Atlantic	6. Gulf of St. Lawrence	Summer feeding	July–Nov	>2000	35	<0.018	<0.012–0.024	During 45 yr of field work, only 35 calves have been sighted	R. Sears (pers. comm., 27 Oct 2023)
Central Indian	7. Southern Sri Lanka	Year-round feeding	Feb–Apr	281	2	0.007	0.001–0.020	Calves noted as being very small	Priyadarshana et al. (2016)
E Indian	8. Bonney Upwelling, SE Australia	Summer feeding	Nov–Apr	1724	50	0.029	0.022–0.038	Size of calf reported on 16 occasions, always noted as a large calf	P. Gill (pers. comm., 15 Nov 2023)
E Indian	9. Perth Canyon	Summer feeding, fall migration	Feb–May	494	11	0.023	0.011–0.038	Data from 25 field seasons 1993–2022, calves are large	V. Sturrock, C. Jenner & M. Jenner (pers. comm., 19 Mar 2024)
E Indian	10. Timor Trough	Winter breeding and feeding	July–Sep	94	8	0.093	0.040–0.161	Surveys with 4512 km of effort during 2007–2008, no sightings mid-Oct to mid-Dec	Burton et al. (2023)
SW Pacific	11. South Taranaki Bight, New Zealand	Summer feeding	Jan–Feb	146	13	0.098	0.053–0.152	Data from 2014, 2016, 2017, of 88 photo-ID individuals, 9 were calves; measured calf lengths were 13.0 and 15.9 m on 5 Feb 2016, with the smaller one nursing	Barlow et al. (2018), L. Torres & D. Barlow (pers. comm., 11 Mar 2023)
Antarctic	12. South of 60° S, 35° E eastwards to 145° W	Summer feeding	Dec–Mar	495	11	0.023	0.011–0.037	JARPA surveys 1987–1988 to 2008–2009	Matsuoka & Hakamada (2020)

tain that they were blue whales. From all strandings with positive species identification and recorded length, only 1 of 176 (0.6%) could have been a fetus. One additional source of information was also uncovered: a pair of studies examining fecal and blubber samples that identified pregnant females through their high progesterone levels, but only 1 of 8 that were resighted the following year were accompanied by calves (Valenzuela-Molina et al. 2018, Atkinson et al. 2020), suggesting either high fetal or calf mortality. Overall, there is some evidence from hormone studies of high fetal or calf mortality but little evidence for fetal mortality from whaling or stranding data.

H3: Low birth rates. Little evidence was uncovered for density-dependent reductions in birth rates since the end of whaling. Most blue whale populations are still recovering from whaling (e.g. Branch et al. 2004), with only those in the northeast Pacific estimated to be approaching pre-whaling numbers (Monnahan et al. 2015). Furthermore, baleen whale populations maintain high rates of increase over a wide range of population sizes, with little evidence for density-dependent effects while rebuilding (Kanaji et al. 2024). No statistical support for increased pregnancy rates at low population sizes was found in Southern Hemisphere baleen whale species (Mizroch 1981), and the generally low abundance levels of most whale species (Lotze & Worm 2009, Lotze et al. 2011, Magera et al. 2013) would suggest that interspecies competition is not currently a major factor. While climate variability certainly has impacted food availability and birth rates in other species (e.g. Greene & Pershing 2004), no direct evidence exists of links between climate change and lower birth rates in blue whales.

H4: Low calf survival. Only 1 estimate of blue whale calf survival was found: 0.545 (95% CI 0.394–0.688) for the Gulf of California (Ugalde de la Cruz 2015), although this estimate may be biased low if some calves never return to this region. In this population, resighting rates of individuals first sighted as calves are generally lower than those of adults (e.g. Sears et al. 2013). This blue whale calf survival estimate is much lower than that for calves of other baleen whale species, and would result in low or negative population growth rates, which is inconsistent with increasing trends in blue whale populations. In other baleen whale species, calf mortality is considerably higher than 0.545 but always lower than mortality in adults: respectively 0.79 vs. 0.96 to 0.97 in North Atlantic right whales (Reed et al. 2022), 0.875 vs. 0.960 in Gulf of Maine humpback whales (Barlow & Clapham 1997), and 0.759 to 0.850 vs. 0.957 to 0.984 in central

North Pacific humpback whales (Gabriele et al. 2001, Mizroch et al. 2004).

Predation on blue whale calves could reduce calf survival. Only killer whales are known predators of blue whales, and there are multiple accounts of killer whale chases, attacks, and successful predation on blue whales (Tappy 1979, Jefferson et al. 1991, Shaughnessy 2000, Pitman et al. 2007, Ford & Reeves 2008, Gemmell et al. 2015, Ugalde de la Cruz 2015, Totterdell et al. 2022). The percentage of blue whales displaying killer whale rake marks varies among populations. In the northeast Pacific, 20% of blue whales display killer whale rake marks, predominantly (59%) on the leading edge of their flukes, and only 6% of resighted individuals displayed new rake marks, indicating that attacks are focused on young individuals (Corsi et al. 2022). In southeastern Australia, only 3.7% of blue whales displayed rake marks, but off western Australia, 42% had rake marks on their flukes and 12% on their flanks (Mehta et al. 2007). Off New Zealand, no rake marks were observed on the flanks of blue whales (Barlow et al. 2019) nor on any of the more limited number of fluke photographs (D. Barlow pers. comm., 19 Mar 2024). Thus, killer whale predation pressure on blue whale calves could be substantial in some areas and negligible in others.

Additional possible causes of low calf survival could be ship strikes, fishing gear entanglement, and lack of nutrition. No studies were found on the relative survival of calves and adult blue whales from these causes.

H5: Calf behavior and visibility. No papers were found that estimated the visibility of calves compared to mothers in field studies. Off Chile, a mother–calf pair was sighted together on 2 February 2004, then the mother alone on 8 February (for 4 min), and then together again on 20 February (Galletti Vernazzani et al. 2012). The calf was only about half of the mother's length and thus unlikely to be close to weaning. Off California, a mother–calf pair was observed on 24 May 2013 from the air for 44 min, during which time the calf was within 1 mother body length, except for a very brief excursion when a nearby boat departed at high speed and the calf moved 2 body lengths (50 m) away from the mother for <1 min (Smultea et al. 2017, 2022). However, in the Gulf of California, calves are sometimes left alone while the mother is feeding, and lone calves are difficult to sight (D. Gendron pers. comm., 18 Nov 2024). Given the small available sample size, it is not possible to estimate the proportion of time that calves spend away from their mothers at different times after birth.

H6: Mother–calf avoidance of aggregations. Multiple satellite tagging studies have been conducted on

blue whales, but reproductive status has not yet been linked to seasonal movements. The most extensive studies are in the northeast Pacific, where 104 of 182 tags transmitted locations for more than 7 d (Palacios et al. 2019). Typically, blue whales spend the summer feeding off California (Jun–Oct), migrate south from October to December, spend time in the Costa Rica Dome (Dec–Apr), and then migrate north during April to May (Horton et al. 2022). However, northeast Pacific blue whales also occasionally diverge thousands of kilometers from this typical pattern, sometimes skipping migrations or moving to the Gulf of Alaska and towards Hawaii before arriving at the Costa Rica Dome, and many spend their winters in the Gulf of California rather than the Costa Rica Dome (Bailey et al. 2009, Blevins et al. 2022, Johnson et al. 2022), where mother–calf pairs are often found in more nearshore areas than other blue whales (Gendron 2002). Baleen from adult females showed more stable migration patterns than other age and sex classes, although 2 adult females skipped the winter migration one year and in the following year moved to the Costa Rica Dome in winter (Blevins et al. 2022). None of these northeast Pacific studies separately identified pregnant females or mother–calf pairs. Chilean blue whales also displayed widely divergent northward migration, with individuals following paths more than 1000 km apart while traveling from summer feeding aggregations to more dispersed wintering regions (Hucke-Gaete et al. 2018). From the Gulf of St. Lawrence, Canada, 2 long-duration tags on females leaving the summer feeding area showed almost no commonality in their autumn and winter wanderings, which included a wide swathe of the northwest Atlantic (Lesage et al. 2017). From the Azores, 10 blue whales tagged in June moved all combinations of east, west, and north, showing wide dispersal from this winter feeding area and no clear common migratory pathway (Pérez-Jorge et al. 2020). In contrast to studies from these 3 regions, Australian blue whales tagged at the end of their summer feeding season displayed stereotypical and narrowly defined migration routes around the western side of Australia, passing on either side of Timor, and into the Banda and Molucca seas in Indonesian waters, although some tracks did end in other areas including south of Bali and the Timor Trough (Double et al. 2014, Möller et al. 2020). Conversely, 2 southbound blue whales tagged off southwestern Timor in spring (Nov) displayed diverging tracks to regions far south and west of Australia (40–50° S) and were separated by up to 40° of longitude (Mustika et al. 2025). None of the satellite tagging studies have tested concurrently taken

biopsy samples for progesterone levels to determine pregnancy status—as is possible (Atkinson et al. 2020)—and in some cases, mother–calf pairs are deliberately not tagged to reduce disturbance (e.g. Mustika et al. 2025). Thus, while there are insufficient data to conclude whether pregnant females or females with calves prefer to avoid blue whale aggregations, blue whales do disperse widely or migrate across a broad front in many blue whale populations.

Passive acoustics studies of blue whale song also suggest broad dispersal of at least some blue whale populations in winter months. While none of the small sample of satellite-tagged Antarctic blue whales departed from the Antarctic (Andrews-Goff et al. 2022), their song has been recorded in all parts of the Pacific, Atlantic, and Indian oceans during winter months, up to the equator (e.g. McDonald et al. 2006, Širović & Oleson 2022, Branch et al. 2023) and sometimes beyond (Samaran et al. 2019). Songs of other populations have also been reported across wide ocean basins in winter months, suggesting that at least the males (which make these loud songs) are widely dispersed for many blue whale populations in winter (e.g. McDonald et al. 2006, Širović & Oleson 2022, Branch et al. 2023).

H7: Timing of calving and weaning. The conceptual model of the timing hypothesis predicts that the proportion of sexually mature females accompanied by calves is at its highest (35–37%) from mid-June to the end of September (in the Southern Hemisphere) (Fig. 2). This is lower than the assumed birth rate of 42.9% because some births take place out of season, and the model includes calf mortality. After accounting for the proportion of the population that is male or immature, the mother–calf proportion is predicted to peak in late winter (Jun–Oct, 7–9%) and to be at a minimum in late summer (Jan–Mar, 1–3%). The predicted peak in the proportion of mother–calf pairs is later (Jun–Sep) than the peak calving date (1 May), since there is a spread in calving dates, and thus the peak occurs after most mothers have calved but before peak weaning (Oct–Jan). The corresponding predictions for the Northern Hemisphere are a peak in December to March (7–9%) and a trough in July to September (1–3%).

Published studies from field studies generally do not report monthly data that could be used to test the timing hypothesis. However, in the northeast Pacific population, 11 females were sighted with calves in the Gulf of California in winter and spring and resighted in summer of the same year off California (Sears et al. 2013). None of the 11 were still accompanied by calves when resighted, indicating that weaning occurred



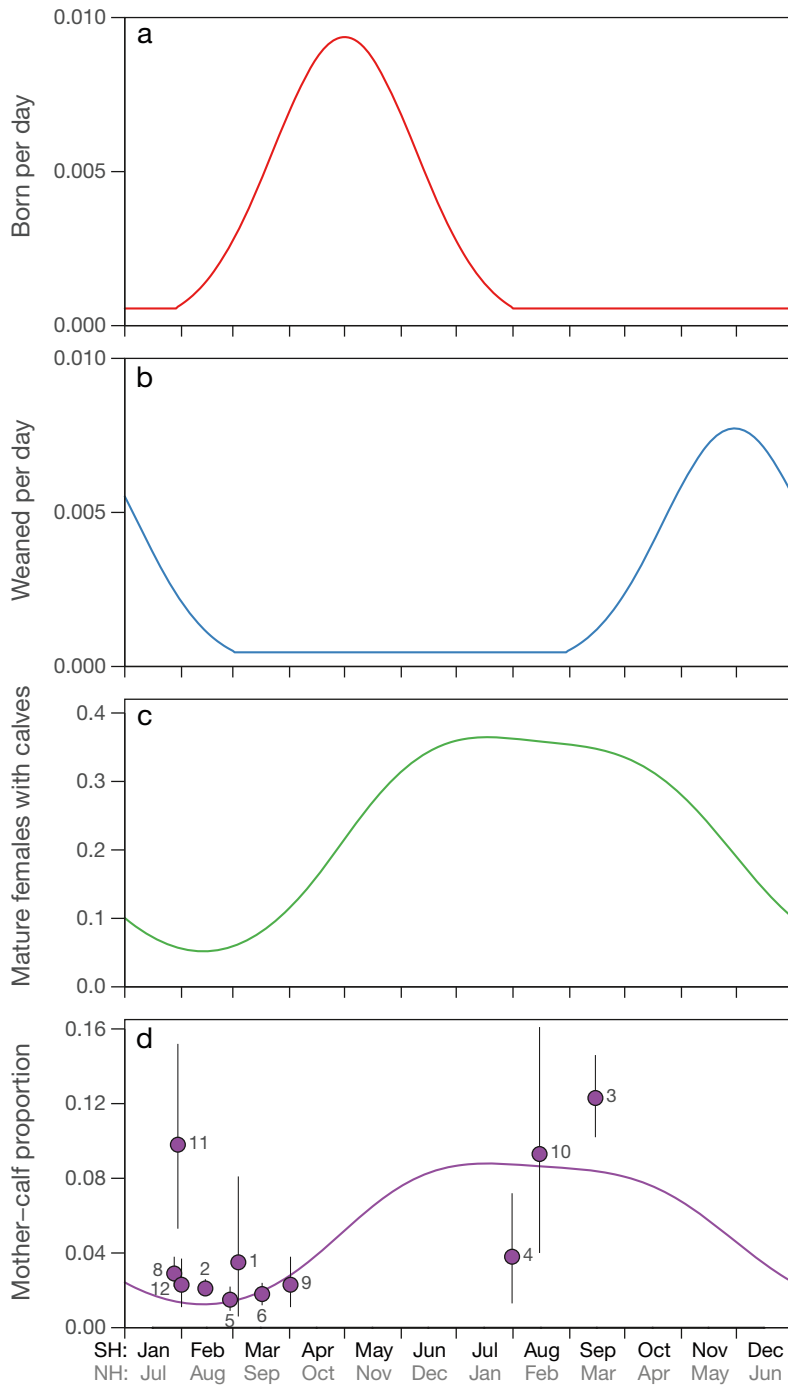


Fig. 2. Timing hypothesis H7 (timing of calving and weaning), with (a) predictions of the proportion of all births that occur on a given day, (b) the proportion of births that survive and are weaned on a particular day, (c) the proportion of sexually mature females that are accompanied by calves on a given day, and (d) the proportion of all sightings that are mother–calf pairs. Observed proportions of sightings that are mother–calf pairs (points at the middle month of the study with 95% CIs) are added to (d), with numbers corresponding to the region labels in Table 1 and Fig. 1. Sri Lanka is excluded (since the breeding season is unclear in this population), the 2 Gulf of California studies are combined, and the 2 southern Chile studies are combined. Months are given for the Southern Hemisphere (SH), with the corresponding Northern Hemisphere (NH) months at the base of the figure in gray

during (or shortly after) their migration to summer feeding regions (Sears et al. 2013).

## 4. DISCUSSION

### 4.1. Compilation of field studies

The compilation of field studies revealed low overall proportions of mother–calf pairs averaging only 3.1% of blue whales across all studies (Table 1). Only 3 of 12 regions (after combining the Chilean studies and the Gulf of California studies) report mean proportions exceeding 4%. The first region, the Gulf of California, with 12.3% mother–calf pairs, is in a winter feeding region (Gendron 2002). The second region, Timor Trough, with 9.3% mother–calf pairs, is in a winter feeding area (Burton et al. 2023) that is also on 1 of the 2 main migration pathways used by pygmy blue whales between Australian and Indonesian waters (Double et al. 2014, Möller et al. 2020). The third region, South Taranaki Bight in New Zealand, has 9.8% mother–calf pairs during summer feeding, although this population is resident there year-round (Barlow et al. 2018). Of the 3 studies conducted in regions inhabited by blue whales in winter, 2 (Gulf of California and Timor Trough) have high observed proportions of mother–calf pairs (12.3 and 9.3%, respectively), while the third region (Galapagos) reported 3.8% mother–calf pairs (Denkinger et al. 2023). The Galapagos has long been assumed to be the wintering grounds for southeast Pacific blue whales from Chile based on satellite tagging and mark–recaptures (Torres-Florez et al. 2015, Hucke-Gaete et al. 2018). However, a photographic mark–recapture also links this region to the Costa Rica Dome north of the equator (Denkinger et al. 2023), where northeast Pacific blue whales travel. Furthermore, northeast Pacific and southeast Pacific blue whales are genetically similar at the subspecies level (Attard et al. 2024).

Thus, it is not completely clear that the Galapagos contains only wintering southeast Pacific blue whales.

#### 4.2. Hypothesis testing

Some of the hypotheses for the low number of observed mother–calf pairs in recent decades can be discarded based on the gathered data, while others require more consideration. Fetuses appear to have high *in utero* survival, not low survival (hypothesis H2). Similarly, there is little support or limited data for low calf survival (H3), low birth rates (H4), or low calf visibility and mother–calf separation before weaning (H5). Therefore, I focus discussion on the proportion of mature females in each population (H1), avoidance of aggregations of blue whales (H6), and the timing hypothesis for calving and weaning (H7).

Hypothesis H1 (accounting for males and immature females) estimates that 7 to 12% of all individuals should be accompanied by calves during the course of a single year. Only in the Gulf of California, Timor Trough, and the South Taranaki Bight (3 of the 12 regions) are the observed proportions in this range. Therefore, this hypothesis is unlikely to explain the low proportion of mother–calf pairs in summer feeding areas.

Hypothesis H6 (mother–calf avoidance of aggregations) cannot be summarily dismissed. Satellite tagging and song detection from passive acoustics show broad dispersal and migration pathways in nearly all blue whale populations. Dispersal in winter makes sense, given the likely important role of killer whale predation in calf mortality, including killer whale predation being one hypothesis for why baleen whales migrate (Corkeron & Connor 1999). Since blue whales flee from killer whales rather than fight them (Ford & Reeves 2008), it also makes sense that they would disperse or travel to areas with a low killer whale presence in winter when accompanied by young calves that cannot yet swim fast enough or long enough to outrun a pod of killer whales. However, satellite tagging has not yet been paired with hormone biopsies to determine whether pregnant mothers or mother–calf pairs migrate differently in winter than unaccompanied females, immature females, or males. An examination of blue whale sex ratios found close to even sex ratios in all areas where blue whales were caught (Branch & Monnahan 2021), although slightly fewer females were caught in Southern Hemisphere winter whaling stations at low latitudes (Saldanha Bay 47.2%, Walvis Bay 47.4%, Durban 46.4%) than at summer whaling stations in the Antarctic (South Georgia 49.8%, South Orkneys 59.8%, South Shet-

lands 55.5%). Thus, it is certainly possible that some mother–calf pairs avoid denser aggregations of blue whales in wintering regions.

Hypothesis H7 invokes the timing of calving and weaning (Fig. 1). The particular values chosen for the conceptual model of this timing hypothesis are realistic but could certainly be refined with additional analysis. Predictions from the timing hypothesis are close to the observed data for 7 of 8 summer feeding regions, which range from 1.5% (combined Chile studies) to 3.5% in the International Whaling Commission's Pacific Ocean Whale and Ecosystem Research surveys covering the North Pacific (albeit with wide CIs from 0.6 to 8.1%). The main exception is the 9.8% in the South Taranaki Bight off New Zealand (Barlow et al. 2018), especially since this relatively high rate was observed in summer (Jan–Feb) at the predicted lowest point for mother–calf presence. This high New Zealand proportion is especially puzzling, given the presence of large fetuses (4–6 m) in whaling data in this region in April to May (Barlow et al. 2023). New Zealand blue whales are unusual in two ways, their year-round presence in New Zealand waters (Barlow et al. 2018) and the absence of killer whale rake marks (Barlow et al. 2019), but it is not clear why either factor should result in relatively high observed proportions of mother–calf pairs. One possibility is that mother–calf pairs congregate more in the South Taranaki Bight—closer to shore than in other parts of their range. In other regions, mother–calf pairs have been more commonly sighted relatively close to shore. Notably, in southern Chile, one study sighted a high proportion (7.9%) of mother–calf pairs, and involved effort concentrated in the interior waters of the Gulf of Corcovado (Hucke-Gaete et al. 2004, 2005), while another study found a very low proportion (0.2%) in offshore waters (Galletti Vernazzani et al. 2012). Similarly, in the Gulf of California, mother–calf pairs are sighted more frequently in calmer, more nearshore waters of the interior Gulf than in the offshore waters of Baja California (Gendron 2002, SEMARNAT 2018). However, the South Taranaki Bight is not particularly sheltered compared to the Gulf of Corcovado or the Gulf of California.

For the three winter regions, the timing hypothesis is consistent with high observed proportions of mother–calf pairs in the Gulf of California (12.3%) (Gendron 2002, Sears et al. 2013) and the Timor Trough (9.3%) (Burton et al. 2023), but observed proportions are well below predictions around the Galapagos Islands (3.8%) (Denkinger et al. 2023), albeit still higher than all of the summer feeding areas except New Zealand. As pointed out earlier, the Galapagos

may include northeast Pacific blue whales among the overwintering southeast Pacific blue whales (Denkinger et al. 2023, Attard et al. 2024), complicating predictions; in addition, some mother–calf pairs may have not been reported, given the opportunistic nature of the Galapagos compilation (Denkinger et al. 2023).

One final anomalous final study region is off Sri Lanka in February to April, where a very low proportion (0.7%) of sightings were mother–calf pairs (Priyadarshana et al. 2016). Sri Lanka blue whale distribution is driven more by the monsoon seasons than by the northern summer and winter (Anderson et al. 2012), and blue whales are present here year-round (Liyanage et al. 2023), albeit with song detections off Oman (Cerchio et al. 2023), Seychelles (Stafford et al. 2023), and the southern Indian Ocean (Samaran et al. 2013). The breeding season of northern Indian Ocean blue whales is also complicated (Mikhalev 2000, Cerchio et al. 2020).

### 4.3. Future directions

Of the hypotheses examined, the timing hypothesis (H7) provides the most promise for prediction, refinement, and future testing. The underlying premise of this model is that shortly after blue whales depart from their summer feeding grounds, pregnant individuals give birth and nurse their calves for about 7 mo, weaning them at about the same time as they return to their summer feeding grounds the following year. In addition to estimating and refining the values used to create the conceptual model and fitting the conceptual model to data to estimate parameters, the following lines of research can be used to test the predictions of the model:

1. Obtain mother–calf proportions from other regions including the Azores and Iceland and expand the datasets from the existing regions.
2. Examine fetal data from whaling records for each population (where available) to estimate the peak calving date, uncertainty around the peak, and variability in timing among populations.
3. For each long-term study area, test the model predictions with observed proportions of mother–calf pairs by day of the year. For summer feeding areas, the conceptual model predicts rapidly declining proportions as the season progresses from November to February (Southern Hemisphere) and from May to August (Northern Hemisphere).
4. Obtain estimates of calf size by day of the year from sightings (particularly from aerial observations) to see if these match the sizes expected from

growth models and dates of birth and weaning. More data may be available for the ratio of calf:mother length than for calibrated absolute calf body length, and both measures could be used to estimate the approximate age of calves to compare against the predictions of the timing hypothesis.

















### 4.4. Implications for other cetacean species

Might the timing hypothesis apply to other species? There is no systematic comparison of observed mother–calf proportions across species, but it is likely that there is a major difference between fight and flight species (Ford & Reeves 2008). In the fight species, breeding is usually in nearshore aggregations (Ford & Reeves 2008), and mother–calf pairs are easily observed at the surface, notably in North Atlantic and southern right, humpback, and gray whales (Gabriele et al. 2001, Perryman et al. 2002, Browning et al. 2010, Brandão et al. 2023). Fight species likely also have later timing of calving after reaching winter aggregations, and possibly prolonged weaning periods (Lockyer 1984), so that mother–calf pairs can be sighted in both summer and winter regions. In contrast, flight species are more dispersed in offshore habitats in winter (Ford & Reeves 2008), may give birth earlier, and have shorter weaning periods (Lockyer 1984). Other flight species besides blue whales might therefore also have few observations of mother–calf pairs compared to pregnancy rates. Notably, Antarctic minke whales *Balaenoptera bonaerensis* have a pregnancy rate of 78% yr<sup>-1</sup> (Best 1982), but weaning is 4 to 6 mo after birth (Williamson 1975, Best 1982), and almost no mother–calf pairs are sighted in summer (Kasamatsu et al. 1988). Indeed, a similar timing hypothesis to the one in this paper has been proposed to explain the low summer sighting rate of Antarctic minke whale mother–calf pairs (Kato 1995).

*Acknowledgements.* The impetus for this project arose from a long conversation with R. Sears, where he highlighted how few calves have ever been encountered in the Gulf of St. Lawrence. Many scientists graciously provided background information and discussion on calves sighted during their in-depth and long-term blue whale studies in different places around the world, including D. Barlow, C. Beck, C. Burton, J. Calambokidis, A. de Vos, J. Denkinger, K. Edyvane, B. Galletti Vernazzani, P. Gill, R. Hucke-Gaete, C. Jenner, P. L. Mustika, R. Sears, V. Sturrock, and L. Torres. Additional information was provided by A. Pande and A. Szesciorka. The manuscript also benefited from discussions and editorial feedback from Z. Rand and K. Randrup and thorough reviews from P. Clapham, D. Gendron, and 1 anonymous reviewer.

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St. Andrews, UK*

*Reviewed by: D. Gendron, P. J. Clapham, R. Harcourt*

*Submitted: September 22, 2024; Accepted: December 13, 2024*

*Proofs received from author(s): February 10, 2025*

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