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Age- and sex-specific survivorship of the Southern Hemisphere long-finned pilot whale (*Globicephala melas edwardii*)

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Biodiversity loss is a major global challenge of the 21st century. Ultimately, extinctions of species are determined by birth and death rates; thus, conservation management of at-risk species is dependent on robust demographic data. In this study, data gathered from 381 (227 females, 154 males) long-finned pilot whales (*Globicephala melas edwardii*) that died in 14 stranding events on the New Zealand coast between 2006 and 2017 were used to construct the first age- and sex-specific life tables for the subspecies. Survivorship curves were fitted to these data using (1) a traditional maximum likelihood approach, and (2) Siler's competing-risk model. Life table construction and subsequent survival curves revealed distinct differences in the age- and sex-specific survival rates, with females outliving males. Both sexes revealed slightly elevated rates of mortality among the youngest age-classes (<2 years) with postweaning mortality rates decreasing and remaining relatively low until the average life expectancy is reached; 11.3 years for males and 14.7 years for females. Overall (total) mortality is estimated to be 8.8% and 6.8% per annum for males and females, respectively. The mortality curve resembles that of other large mammals, with high calf mortality, lower postweaning mortality, and an exponentially increasing risk of senescent mortality. An accelerated mortality rate was observed in mature females, in contrast to the closely related short-finned pilot whale (*G. macrorhynchus*), which selects for an extension to the postreproductive life span. The reason for the observed differences in the mortality rate acceleration and postreproductive life span between the two pilot whale species have not been established and warrant further investigation. Obtaining robust information on the life history of long-lived species is challenging, but essential to improve our understanding of population dynamics and help predict how future pressures may impact populations. This study illustrates how demographic data from cetacean stranding events can improve knowledge of species survival rates, thus providing essential information for conservation management.

Key words: age estimation, cetacean, conservation, demography, life history, life tables, marine mammal, population parameters, Siler model, survivorship

Given the unprecedented rates of biodiversity loss globally, evidence-based conservation policies are urgently required (Conde et al. 2019; Almond et al. 2020). Birth and death rates set the pace of population increase or decline and drive the expansion or extinction of a species. Therefore, demographic data are essential to inform species conservation policies and develop risk assessments (Conde et al. 2019). Life tables and survivorship curves have proven to be powerful conservation tools when combined with demographic models that predict the susceptibility of certain age-classes to anthropogenic impacts (e.g., Crouse et al. 1987; Moore and Read 2008).

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Models of population viability are fundamentally based on age structure (Caughley 1977; Barlow and Boveng 1991). Determining the age structure of a population is, therefore, the essential first step when studying population dynamics (Evans and Hindell 2004). Further, the parameters that have been interpreted to reflect significant changes to population abundance or resource availability are those specific to age, for example, age at sexual maturation, age-specific fecundity rates, and growth parameters of individuals in the population (Caughley 1977; Evans and Hindell 2004). Additionally, determining age-at-death of individuals removed by anthropogenic activities (e.g., drive fisheries or fisheries bycatch), or mass mortality events, is crucial not only for understanding the dynamics of a population, but also for determining if particular ontogenetic groups are more or less at risk.

Survival and mortality rates can be inferred directly by following one or more cohorts through time, or indirectly from analysis of age distribution of live (Caughley 1966; Barlow and Boveng 1991) or dead (Caughley 1966; Stolen and Barlow 2003) individuals. All methods involve assumptions that are unlikely to be fully satisfied but are often estimated well enough for practical purposes (Stolen and Barlow 2003). Life tables based on age-at-death data have been presented for several species of large terrestrial mammals (e.g., Caughley 1966; Laws 1968; Spinage 1972). However, obtaining robust estimates of survival probabilities for cetacean populations remains challenging, and published examples of age-structured life tables are rare (Barlow and Boveng 1991; Stolen and Barlow 2003).

In cetaceans, changes at the population level can occur due to stressors such as climate change, pollution, fishery-related activities, noise pollution, disease, and habitat degradation, and populations can vary in their ability to recover (Simmonds 2018). For most cetacean species, stranding records provide the most accessible source of information about the population dynamics (Saavedra 2018). When stranding records are examined, four main types of strandings can be identified: (1) single strandings, (2) mass-stranding events (MSEs), (3) mass mortalities and unusual mortality events (UMEs), and (4) out of habitat situations (Moore et al. 2018). The majority of these events are single strandings, involving individuals that have either become ill or died before coming ashore, but occasionally large groups of apparently healthy cetaceans strand live. Most cetaceans involved in an MSE often die in situ or a short distance away from the original stranding site (Martin et al. 1987). It is not understood why apparently healthy cetaceans strand en masse, although there are a variety of both natural and anthropogenic hypotheses including coastal topography and oceanography (Brabyn and McLean 1992; Walker et al. 2005; Brownlow et al. 2015; Hamilton 2018), meteorological and geomagnetic conditions (Evans et al. 2005; Bradshaw et al. 2006; Mazzariol et al. 2011), seismic activity, and sonar noise (Fernandez et al. 2005; Southall et al. 2006, 2013; Brownlow et al. 2015). It is likely that a number of factors contribute to each stranding event, and these vary on a case-by-case basis. MSEs should not be confused with mass mortality events or UMEs where animals strand dead (or dying) over an extended period of time (Moore et al. 2018).

The long-finned pilot whale (LFPW; *Globicephala melas*) is among the species most often involved in live MSEs throughout their range (Minton et al. 2018). Pilot whales tend to strand in large numbers of mixed ages and sexes on gently sloping beaches, and strandings often recur in a specific geographic area: for example, Cape Cod, Massachusetts, United States (McFee 1990; Wiley et al. 2001; Sweeney et al. 2005); Tasmania, Australia (Evans et al. 2005; Kemper et al. 2005; Gales et al. 2012; Beasley et al. 2019); and Golden Bay, New Zealand (Betty et al. 2020). Although the cause(s) of MSEs is often not determined (e.g., Bogomolni et al. 2010; Dolman et al. 2010), there is no doubt that strong social bonds exist within pilot whale groups (Olson 2018). Given that the mass-stranded groups of LFPWs have been found to reflect the age and sex composition of entire pods driven ashore by fisheries (Sergeant 1982), and there is usually no reason to suspect that live mass-stranded groups are unrepresentative of free-ranging pods (Martin et al. 1987), MSEs provide a valuable opportunity to study the demography of the species.

The current study investigated the age structure, and age and sex-specific survivorship and mortality, of the Southern Hemisphere subspecies of LFPW, *G. m. edwardii*. Specifically, we present age- and sex-specific (1) life tables, (2) survivorship curves, and (3) mortality schedules for *G. m. edwardii* using age-at-death data collected from animals that did not survive stranding events on the New Zealand coast between 2006 and 2017.

Materials and Methods

Age estimation.—Teeth from 405 LFPWs (239 females, 163 males, and three of unknown sex) that died in 14 stranding events on the New Zealand coast between 2006 and 2017 were collected for age estimation purposes (Table 1). Sex was determined by gross examination of external genital opening. Age estimation was performed by counting annual growth layer groups (GLGs) in decalcified and stained longitudinal sections of teeth, as described by Perrin and Myrick (1980). Tooth preparation methods for this study were adapted from Lockyer (1993), and all sections were read by at least two individuals (for further explanation, see Betty et al. 2022). Individuals for which age could not be estimated reliably were excluded from further analysis. Ages from a total of 381 whales from 14 stranding events (median 19.5, range 1–95 per stranding event), including 227 females (median 11.5, range 0–64 per stranding event) and 154 males (median 9, range 0–31 per stranding event), were used to construct age- and sex-specific life tables, as detailed below.

Calves that did not possess a neonatal line in the tooth, or had a neonatal line forming, with no additional postnatal dentin, were classified as newborns. Individuals were considered weaned if they were older than 2 years, sexually immature if they were younger than the estimated age at attainment of sexual maturity (ASM) for the population, or sexually mature if they were older than or equal to the estimated ASM, that is, 13.5 and 6.7 years for males and females, respectively (Betty 2019; Betty et al. 2019).

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Table 1.—Sex and maturity composition of long-finned pilot whales (*Globicephala melas edwardii*) that did not survive stranding on the New Zealand coast (2006–2017), by stranding event. No. strand = total number of whales involved in stranding event; No. dead = total number of whales that died during the stranding event; IF = immature female (< estimated attainment of sexual maturity [ASM] of 6.7 years; see Materials and Methods section); IM = immature male (< estimated ASM of 13.5 years; see Materials and Methods section); MF = mature female (≥ASM); MM = mature male (≥ASM); UK = unknown sex-maturity category.

Date	Location	No. strand	No. dead	IF	IM	MF	MM	UK
12 December 2006	Muriwai, Auckland	1	1	0	0	0	1	0
23 January 2008	Farewell Spit, Golden Bay	34	14	2	2	2	2	6
25 December 2009	Farewell Spit, Golden Bay	105	105	15	14	19	12	45
23 January 2010	Port Levy, Banks Peninsula	54	16	7	5	4	0	0
14 February 2010	West Ruggedy Beach, Stewart Island	28	28	2	6	8	3	9
18 June 2010	Ruapuke, Waikato	20	20	3	4	9	4	0
22 September 2010	Te Horo Beach, Far North	49	40	5	6	20	7	2
4 February 2011	Port Puponga, Golden Bay	84	17	0	4	2	1	10
20 February 2011	Mason Bay, Stewart Island	107	107	14	17	50	14	12
14 November 2011	Farewell Spit, Golden Bay	65	65	3	11	23	7	21
6 January 2014	Farewell Spit, Golden Bay	39	39	4	13	16	3	3
14 January 2014	Farewell Spit, Golden Bay	99	98	0	5	15	4	74
3 November 2014	Muriwai, Auckland	1	1	1	0	0	0	0
10 February 2017	Farewell Spit, Golden Bay	600	200	1	6	2	3	188
		1,286	751	57	93	170	61	370

Life tables, survivorship, and mortality rates.—Life tables, including age-specific survivorship (l_x) and mortality (q_x) rates for both male and female LFPWs, were constructed using two approaches: (1) following the traditional approach as described by Caughley (1966) and Krebs (1989), and (2) fitting the Siler competing-risk model (Siler 1979; Barlow and Boveng 1991; Bloch et al. 1993a; Stolen and Barlow 2003; Moore and Read 2008) to smooth the age-at-death data. The life table calculations for both the traditional and Siler methods were constructed using estimated ages and are based on a hypothetical cohort of 1,000 LFPWs. In order to construct these life tables, it was assumed that (1) MSEs of LFPWs on the New Zealand coast are representative of the population, (2) carcass recovery and tooth collection from MSEs were independent of age and sex, and (3) the population has a stable age distribution and a zero-growth rate (often referred to as a stationary age distribution; Caughley 1966).

Traditional life tables have previously been applied to stranded cetaceans (e.g., Stolen and Barlow 2003; Evans and Hindell 2004; Murphy et al. 2007) where theoretical populations are constructed with corresponding abundance by age. Vectors of age-specific survival and mortality are then estimated from this population structure using the traditional method as given by Krebs (1989), where: n_x = the number of individuals alive at age x; d_x = the number of individuals dying during the age interval x to $x + 1$; l_x = the proportion of the animals surviving to the start of age x (i.e., survivorship); q_x = the proportion of animals alive at age x that die before age $x + 1$ (i.e., mortality rate); e_x = average (remaining) life expectancy for individuals at age x; $\sum d_x / \sum l_x$ = overall (total) annual average mortality rate.

Mortality and survival rates directly derived from observational age-at-death data are generally imprecise and may be biased (e.g., underrepresentation of young ages) and therefore model-based estimates are preferred (Saavedra 2018). In this study, the Siler model (Siler 1979) was used to smooth the age-at-death data, and avoid violating the requirements of a vertical life table (i.e., that the frequency of each age-class x is equal to or greater than age-class $x + 1$). The Siler model (Siler 1979) was selected over the commonly used Gompertz model (Gompertz 1825) because the Siler model does not require any assumption on when the onset of aging occurs and therefore retains the expected relationships between juvenile, adult, and senescent life stages (Saavedra 2018; Lemaître et al. 2020). The Siler model adequately fits expected mortality patterns for a wide range of long-lived species, including marine mammals (Barlow and Boveng 1991; Stolen and Barlow 2003; Mannocci et al. 2012; Saavedra 2018; Lemaître et al. 2020). In the Siler model, survivorship at a given age $l(x)$ is expressed as the product of three competing risks as denoted in equation (1).

$$l(x) = l_j(x) \times l_c(x) \times l_s(x) \tag{1}$$

where: $l_j(x) = exp\{(a_1/b_1)[1 - exp(-b_1 x)]\}$ is an exponentially decreasing risk due to juvenile risk factors; $l_c(x) = exp\{-a_2 x\}$ represents a constant risk experienced by all age-classes; $l_s(x) = exp\{(a_3/b_3)[1 - exp(b_3 x)]\}$ is the exponentially increasing risk due to senescence; x is a given age and a_n and b_n are the Siler parameters. The total mortality at a given age $\mu(x)$ is the sum of the juvenile mortality $\mu_j(x)$, the constant mortality affecting all age-classes $\mu_c(x)$, and the senescent mortality $\mu_s(x)$, as denoted in equation (2).

$$\mu(x) = \mu_j(x) + \mu_c(x) + \mu_s(x) \tag{2}$$

Total mortality can be calculated using the Siler parameters $(a_1, b_1, a_2, a_3, b_3)$ as denoted in equation (3).

$$\mu(x) = a_1 \, exp\,(-b_1 x) + a_2 + a_3 \, exp(b_3 x) \tag{3}$$

The above equation describes the general shape of the mortality curve using five parameters that account for initially increasing (and subsequently decreasing) risk of an individual dying at the beginning of life, a constant risk through life,

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and increased risk due to senescence. The competing-risk Siler model was fitted to the LFPW age-at-death data using the Nelder and Mead (1965) optimization method implemented in the "strandCet" package (Saavedra 2018) in R (R Development Core Team 2018).

Results

Age structure.—Age was estimated for 227 female and 154 male LFPWs (Fig. 1) stranded in 14 independent events (Table 1). Age ranges or a minimum age were obtained from a further 22 whales due to difficulties in counting GLGs in their dentin and cementum; these individuals were not included in the subsequent life table construction. Females ranged from 0 to 38 years and males from 0 to 31 years (Fig. 1). The age-specific male sample was composed of younger individuals than the female sample, with 28% of males younger than 5 years and 90% younger than 20 years, compared with 18% of females younger than 5 years and 71% younger than 20 years. Overall, the data set was dominated by sexually immature individuals of both sexes (n = 150) and sexually mature females (n = 170) with a smaller number of mature males (n = 61; Table 1) and very few males older than 20 years (n = 12; Fig. 1).

Life tables, survivorship, and mortality rates.—Life table construction (Supplementary Data SD1–SD3) and subsequent survival (Fig. 2) and mortality curves (Fig. 3) showed distinct differences in the age- and sex-specific survival and mortality rates for New Zealand LFPWs. The traditional life table (Supplementary Data SD1) estimates the average life expectancy at birth to be 13.6 years, while the sex-specific model life tables estimate average life expectancy to be 11.3 years and 14.7 years for males and females, respectively (Supplementary Data SD2 and SD3). Males exhibited much lower postweaning (>2 years) survival rates than females (Fig. 2).

Using data from the traditional life table (Supplementary Data SD1), the overall (total) mortality for the population of LFPWs in New Zealand waters is estimated to be approximately 7.3% per annum. Using data from the sex-specific model life tables (Supplementary Data SD2 and SD3), the overall (total) mortality is estimated to be 8.8% and 6.8% per annum for males and females, respectively. Both sexes showed slightly elevated rates of mortality among the youngest age-classes (<2 years) with postweaning mortality rates decreasing and remaining low until 11 years of age for males and 15 years of age for females (Supplementary Data SD2 and SD3; Fig. 3). Following which, mortality rates increase sharply in adult males and more gradually in adult females (Fig. 3).

Discussion

Firstly, it must be acknowledged that the demographic data presented in this study have been collected solely from stranding events, which may not provide a true representation of the stable age distribution of the population. Stranded groups may represent subgroups rather than the entire pod, resulting in some individuals being missed in the sample by chance. It also is possible that some demographic subgroups are less likely to strand en masse, or more likely to survive stranding events and were therefore not sampled (Betty et al. 2022). In this study, age and sex were not always determined for all individuals in large MSEs (Table 1). While this potential bias cannot be ignored, this study is based on a large, minimally biased sample (i.e., particular ontogenetic groups were not favored, except 2 out of 12 MSEs where adult males were targeted for gonadal sampling; see Betty et al. 2019) that likely reflects

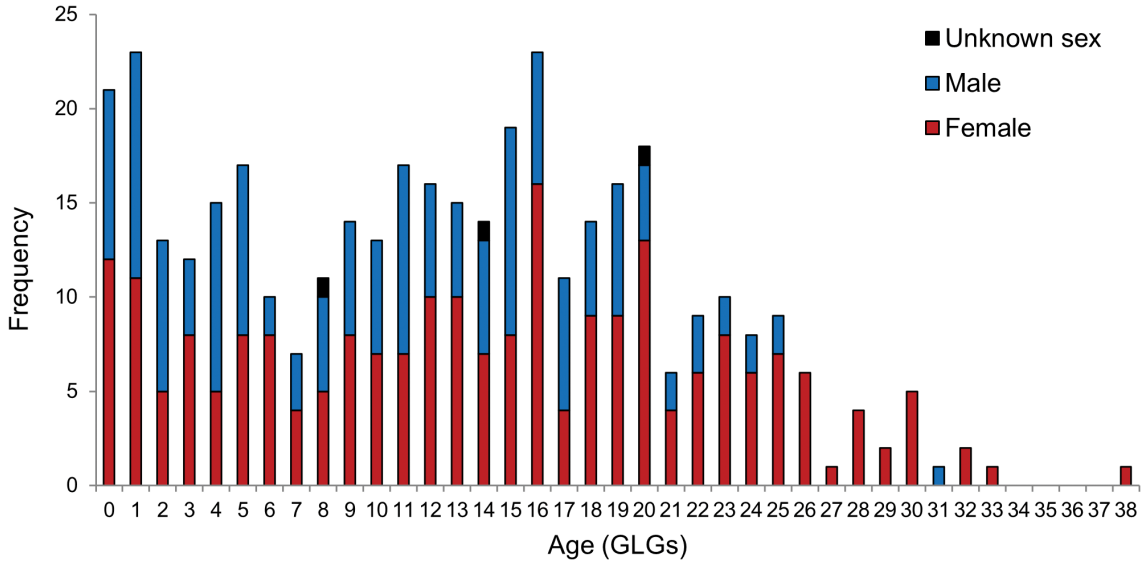

Fig. 1.—Age distribution of female (n = 227), male (n = 154), and unknown sex (n = 3) long-finned pilot whales (*Globicephala melas edwardii*) mass-stranded on the New Zealand coast between 2006 and 2017.

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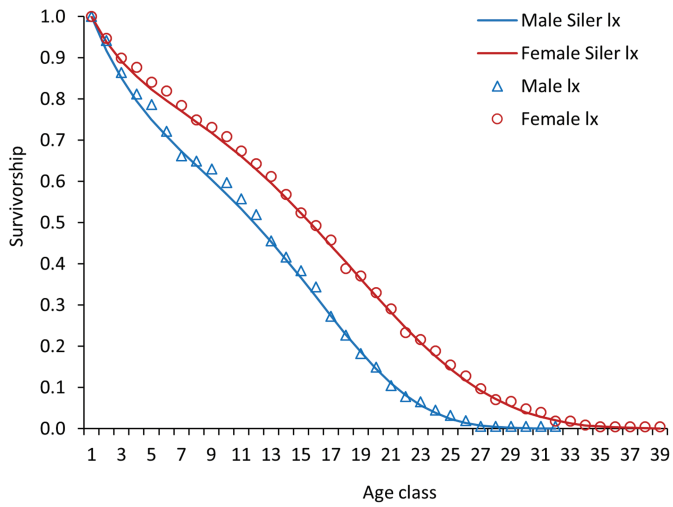

Fig. 2.—Age-specific survivorship (*lx*) for male and female long-finned pilot whales (*Globicephala melas edwardii*) mass-stranded on the New Zealand coast between 2006 and 2017. Points are based on traditional life table calculations (*lx*) and smoothed curves were fitted using the Siler model (Siler *lx*). Age-class = age *x* to *x* + 1.

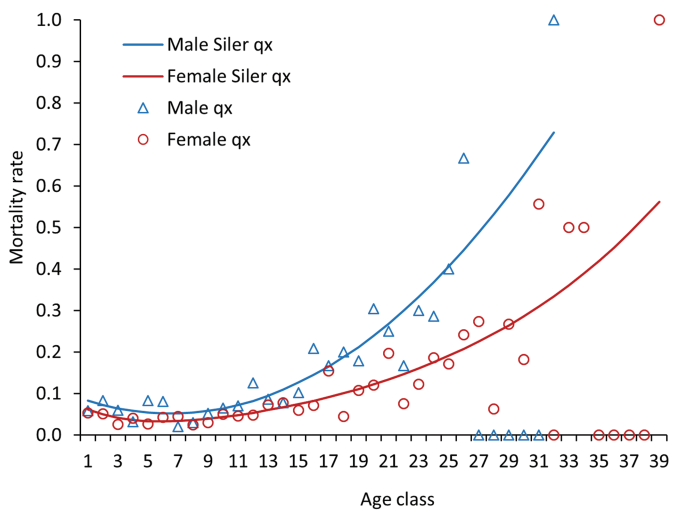

Fig. 3.—Age-specific mortality rates (*qx*) for male and female long-finned pilot whales (*Globicephala melas edwardii*) mass-stranded on the New Zealand coast between 2006 and 2017. Points are based on traditional life table calculations (*qx*) and smoothed curves were fitted using the Siler model (Siler *qx*). Age-class = age *x* to *x* + 1.

the true age distribution of the MSEs, and also the local New Zealand population (Betty 2019). In a New Zealand context, mass-stranded LFPW groups are biased toward females, particularly within the adult age-classes, while a male bias is reported in juveniles (Betty 2019; Betty et al. 2020). However, the predominance of females also appears to be a common observation in groups of both captured (Sergeant 1962, Bloch et al. 1993b) and mass stranded (Martin et al. 1987; Betty et al. 2020; Ball et al. 2022) LFPWs globally. Despite potential selection bias with data derived from stranded individuals, the frequent MSEs of LFPWs on the New Zealand coast (in large groups of mixed ages and sexes; see Table 1 and Betty et al. 2020) provides a valuable opportunity to collect demographic data.

Age structure.—The age structure of any population of animals at a given point in time is a factor of mortality and recruitment into that population. The age-specific data set of LFPWs stranded on the New Zealand coast comprised immature and mature individuals of both sexes, though among the matures there were many more females than males (Table 1). The sample of stranded LFPWs in this study, and therefore the "population" from which survival was estimated, resulted in different age structures for males and females, with very few (n = 12) males older than 20 years of age (Fig. 1).

The small proportion of males greater than 20 years in this dataset may be the result of older (mature) males being less likely to strand (or having a higher refloat success than other ontogenetic groups), possibly as a consequence of (1) the dispersal of older (mature) males from natal groups into male-only groups and/or (2) forming temporary associations with other matrilineal groups for breeding (Betty et al. 2019). Mature males may be unlikely to suffer MSE-related mortality when in groups other than their natal group (due to social bonds not being established or reinforced). In addition, if male-only groups of LFPWs inhabit waters further offshore, they would be less likely to encounter land and subsequently strand, and they would also be unencumbered by calves and juveniles.

Based on limited genetic evidence, it has been proposed that while male LFPWs mostly remain within their natal group, they do not father calves within the group, suggesting at least some temporary male dispersal for mating purposes (Amos et al. 1993). Within the North Atlantic, occasional observations of male-only LFPW groups have been reported (Sergeant 1962, Bloch 1992, Desportes et al. 1993) and the occurrence of "bachelor groups" have been well-documented in another odontocete species, the sperm whale *Physeter macrocephalus* (Best 1979; Jaquet et al. 2000; Lettevall et al. 2002). Male dispersal could potentially explain the prevalence of females in groups of both captured (Sergeant 1962, Bloch et al. 1993b) and mass stranded (this study; Martin et al. 1987; Betty et al. 2020; Ball et al. 2022) LFPWs. For *G. m. edwardii*, this is difficult to confirm due to the lack of observational and other available data on the subspecies. Further molecular studies, using samples collected from complete groups are required to enable a thorough assessment of the social structure of the species. However, there is some genetic evidence that MSEs of LFPWs on the coasts of Scotland, Tasmania, and New Zealand can contain multiple matrilines in a single event (Oremus et al. 2013; Ball et al. 2022). Thus, it has been suggested that both LFPW subspecies form associations comprising multiple matrilineal groups (Oremus et al. 2013; Ball et al. 2022), as also supported by behavioural studies of *G. m. melas* in the north-west Atlantic (Ottensmeyer and Whitehead 2003; Augusto et al. 2017).

Alternatively, these stranding data may be representative of the population, with higher (natural or anthropogenic) mortality in males relative to females for all or part of their life span, resulting in females outnumbering males of a similar age (especially in adulthood). Reduced longevity of males, relative to their female conspecifics, is a common feature of mammalian

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populations, including LFPWs (Betty et al. 2022), and may be influenced by the interactions between sex-specific costs of sexual selection and local environmental conditions (Lemaître et al. 2020). In cetaceans, these include costs associated with social structure and sex differences in ranging patterns (Stolen and Barlow 2003), and mate selection in polygynous mating systems (Ralls et al. 1980). If male LFPWs do indeed emigrate from their natal group (and move between groups), males that travel alone or in small groups may be more vulnerable to predation (Stolen and Barlow 2003). Male LFPWs also display significant sexual size (males larger than females) and shape dimorphism, potential fitness-related traits that are energetically costly and associated with mate selection (Bloch et al. 1993c; Betty et al. 2022).

It is also possible that higher male mortality may be related to disease and/or pollutant burden. For example, sharp decreases in survival probabilities have been reported for *G. m. melas* in the Strait of Gibraltar following morbillivirus epizootics, which have also been linked to high organochlorine (OC) contaminant concentrations in this population (Lauriano et al. 2014, Pons et al. 2022). These morbillivirus outbreaks have been observed to affect sexes differently, with male LFPWs showing a more severe decrease in survival rate compared to females (Pons et al. 2022). This finding supports the idea that high OC concentrations could affect immunity, with females being less affected due to their ability to offload contaminants through pregnancy and lactation (Aguilar and Borrell 1988). With the exception of a recent study examining trace element concentrations (Lischka et al. 2021), very little information is available on the pollutant burden of *G. m. edwardii* in New Zealand waters. Further investigation is required to examine current levels of organochlorine and other emerging contaminants in *G. m. edwardii* and to identify any population-level impacts.

Life tables, survivorship, and mortality rates.—Methods of estimating mortality rates from age-at-death data assume that age-specific fecundity and mortality are stable and that the exponential rate of increase has been, and is currently, zero (Caughley 1966; Caughley and Sinclair 1994; Evans and Hindell 2004). This assumption is difficult to validate—the age structures of real populations are often not stable, resulting in differing amounts of variation around life table parameters. To account for this variation, Caughley (1977) proposed a minimum sample size of 150 for accurately estimating survival. It is often difficult to obtain such large sample sizes for cetaceans but it was possible in this study due to the high frequency of LFPW MSEs on the New Zealand coast (Betty et al. 2020). Further, long-lived species such as delphinids are buffered from perturbations from stable age distribution due to their long reproductive period and high rates of survival (Stolen and Barlow 2003). The age-at-death data reported here are based on an 11-year time series that also acts to average out the deviations that might be present in any given year.

In populations that are not stationary, vertical estimates of survivorship (i.e., based on the age structure of a population at a specific point in time) overestimate mortality rates when compared to those derived from a horizontal perspective (i.e., based on the fate of a cohort followed through time; Olesiuk et al. 1990; Evans and Hindell 2004). Apparent changes in the mortality of older groups are influenced not only by the deaths of older individuals but also by changes in the initial sizes of cohorts through time. The extent of this bias is a function of the true mortality rate and the population growth rate (Evans and Hindell 2004). It is recognized that the survival and mortality rates presented here are tentative; nevertheless, they still provide a basis for relative comparisons between (sub)species and populations.

The overall survival curve for *G. m. edwardii* in New Zealand waters (Fig. 2) is typical of mammals and other long-lived species (Spinage 1972; Stolen and Barlow 2003). The sex-specific survival curves show that females have higher postweaning (Betty 2019) survival rates relative to males after 2 years of age, with the difference being particularly marked around the age of 20 years. Mortality curves created from these life table data using the Siler model (Fig. 3) approximate the typical U-shaped curves of other large mammals (Caughley 1966; Spinage 1972) but with lower than expected mortality in animals younger than 2 years old. Again, there are differences between the sexes with males displaying higher mortality rates in the adult years.

Large differences in mortality with age and sex occur in many mammals. Higher mortality among the very young has been observed in both terrestrial (Caughley 1966) and marine mammals. For example, high neonate mortality has been reported for New Zealand sea lions (*Phocarctos hookeri*, neonatal mortality rate = 0.14; Castinel et al. 2007) and cetaceans such as Atlantic spotted dolphins (*Stenella frontalis*, yearling mortality rate = 0.24; Herzing 1997) and common bottlenose dolphins (*Tursiops truncatus*, yearling mortality rate = male: 0.11 and female: 0.08; Stolen and Barlow 2003). Causes of high calf mortality in cetaceans are difficult to identify, though it is likely that factors such as nutrition, social interactions, predation pressures, and maternal transfer of pollutant load have compounding effects (Stolen and Barlow 2003; Wells et al. 2005). High neonate and calf mortality has been reported for LFPWs (*G. m. melas*) captured in drive fisheries in the Faroe Islands (yearling mortality rate = female: 0.15; Bloch et al. 1993a), but was not as pronounced for SFPWs captured in drive fisheries in Japan (yearling mortality rate = male: 0.10 and female 0.07; Kasuya and Marsh 1984), or stranded LFPWs in the current study (first-year mortality rate = male: 0.08 and 0.06: female). It would usually be expected that the actual proportion of calves dying in the population may be underestimated by the number of single-stranded or beach cast carcasses recorded due to the more rapid decomposition, greater vulnerability to predation, and the lower detection probability of small-sized animals (Stolen and Barlow 2003). However, age data in this study were predominantly obtained from live MSEs, which (although still potentially biased) are likely to be representative of the free-ranging groups (Sergeant 1982).

Overall (total) average annual mortality rates for *G. m. edwardii* (males 8.8% and females 6.8%) are comparable to those previously estimated for *G. m. melas* (males ~8% and females ~7%; Bloch et al. 1993a). However, SFPWs appear

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to have considerably lower overall female mortality rates than LFPWs (total average annual mortality rates: males 8.3% and females 4.5%; Kasuya and Marsh 1984). Female SFPWs caught in Japanese drive fisheries show high juvenile mortality, followed by a period of lower mortality during prime reproductive years, and then a higher mortality rate in the postreproductive or senescent years (>40 years of age; Kasuya and Marsh 1984; Ellis et al. 2018b). In contrast, the results of this study suggest that female *G. m. edwardii* show a pattern of mortality more similar to *G. m. melas*. Both LFPW subspecies do not exhibit a pronounced period of relative stability and low mortality during midlife—rather, they show a relatively stable period of low mortality until their teens, followed by a steady decline with age (in a similar manner to the males; Bloch et al. 1993a; Ellis et al. 2018b).

The greatest decrease in survival rate of mature female *G. m. edwardii* occurred between 20 and 30 years of age (this study), compared to between 30 and 40 years for mature female *G. m. melas* (Bloch et al. 1993a), which may be explained by their relative longevity (i.e., *G. m. edwardii*: 38 years vs. *G. m. melas*: 59 years; Betty et al. 2022). For species that have been reported to live longer, for example, female SFPWs (longevity 64.5 years) and resident killer whales (longevity 80 years), a relatively stable rate of survival was observed during adulthood, followed by a decrease in survival between the ages of 30 and 45 years (Kasuya and Marsh 1984; Olesiuk et al. 1990). However, both SFPWs and resident killer whales appear to have selected for an extension of the postreproductive life span (Foote 2008). The proportion of the adult life span that is postreproductive (postreproductive representation; PrR) is 0.31 in resident killer whales and 0.26 in SFPWs (Kasuya and Marsh 1984; Foote 2008; Ellis et al. 2018a, 2018b). In contrast, no significant PrR (0.002), but rather an acceleration in the mortality rate, is observed in *G. m. melas* (Bloch et al. 1993a; Ellis et al. 2018a, 2018b).

The observed variation in life-history strategies between the two pilot whale species may in part be due to the social organization within stable social groups and the benefits of cooperative foraging and multigenerational transfer of information (Marsh and Kasuya 1984; Whitehead 2015; Ellis et al. 2018b; Betty 2019). The social structure of pilot whale pods is thought to be similar to that of killer whales (Olson 2018) but the reason for the observed differences in the acceleration of mortality rates and postreproductive life spans between the two pilot whale species has not been established (Foote 2008; Ellis et al. 2018b). Other species with longevity closer to *G. m. edwardii* (e.g., common bottlenose dolphins from the Indian River Lagoon system, longevity 35 years; Stolen and Barlow 2003) also do not show a stable period of low mortality during midlife, but instead a gradual decline and greatest decrease in survival between 20 and 30 years. Increases in birth-related mortality, susceptibility to predation due to the care and protection of young and greater energetic demands on females associated with gestation and lactation may affect the survival of females in the later reproductive years, as suggested for sperm whales (Evans and Hindell 2004). Overall, there is still a considerable amount to learn about the interplay between odontocete population dynamics, social structure, and life history.

This 11-year study is the first comprehensive demographic assessment of the Southern Hemisphere LFPW and provides essential information to parameterize future population viability assessments. In a changing world, information on population demography and age- and sex-specific survival rates will be an increasingly important part of conservation status assessments (Arso Civil et al. 2019). Demographic data, when collected in a standardized and comprehensive manner, offer an ability to assess changes in population parameters over time, providing essential information for conservation management. The approach used in this study is broadly applicable to data gathered by stranding networks in other areas. With dedicated collection of life-history samples, similar age- and sex-specific survival models can be developed for other cetacean populations and used to explore the impacts of environmental change.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Life table for both sexes (including unknown sex) of long-finned pilot whale

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(*Globicephala melas edwardii*) based on individuals mass-stranded on the New Zealand coast between 2006 and 2017 (n = 384) and scaled up for a hypothetical population of 1,000 individuals.

Supplementary Data SD2.—Life table for male long-finned pilot whales (*Globicephala melas edwardii*) based on individuals mass-stranded on the New Zealand coast between 2006 and 2017 (n = 154) and scaled up for a hypothetical population of 1,000 individuals.

Supplementary Data SD3.—Life table for female long-finned pilot whales (*Globicephala melas edwardii*) based on individuals mass-stranded on the New Zealand coast between 2006 and 2017 (n = 227) and scaled up for a hypothetical population of 1,000 individuals

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