

LONG TERM STUDY

Patterns, sources, and consequences of variation in age-specific vital rates: Insights from a long-term study of Weddell seals

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Handling Editor: Pol Capdevila**Abstract**

1. Variations in the reproductive and survival abilities of individuals within a population are ubiquitous in nature, key to individual fitness, and affect population dynamics, which leads to strong interest in understanding causes and consequences of vital-rate variation. For long-lived species, long-term studies of large samples of known-age individuals are ideal for evaluating vital-rate variation.
2. A population of Weddell seals in Erebus Bay, Antarctica, has been studied each Austral spring since the 1960s. Since 1982, all newborns have been tagged each year and multiple capture-mark-recapture (CMR) surveys have been conducted annually.
3. Over the past 20 years, a series of analyses have built on results of earlier research by taking advantage of steady improvements in the project's long-term CMR data and available analytical methods. Here, I summarize progress made on four major topics related to variation in age-specific vital rates for females: early-life survival and age at first reproduction, costs of reproduction, demographic buffering, and demographic senescence.
4. Multistate modelling found that age at first reproduction varies widely (4–14 years of age) and identified contrasting influences of maternal age on survival and recruitment rates of offspring. Subsequent analyses of data for females after recruitment revealed costs of reproduction to both survival and future reproduction and provided strong evidence of demographic buffering. Recent results indicated that important levels of among-individual variation exist in vital rates and revealed contrasting patterns for senescence in reproduction and survival.
5. Sources of variation in vital rates include age, reproductive state, year, and individual. The combination of luck and individual quality results in strong variation in individual fitness outcomes: ~80% of females born in the population produce no offspring, and the remaining 20% vary strongly in lifetime reproductive output (range: 1–23 pups).
6. Further research is needed to identify the specific environmental conditions that lead to annual variation in vital rates and to better understand the origins

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of individual heterogeneity. Work is also needed to better quantify the relative roles of luck, maternal effects, and environmental conditions on variation in vital rates and to learn the importance of such variation to demographic performance of offspring and on overall population dynamics.

KEYWORDS

Antarctica, life-history evolution, long-term studies, population biology, vital rates, Weddell seals

1 | INTRODUCTION

An organism's key life-history traits include the distribution of survival rates and reproductive effort by age, costs of reproduction to future survival and fecundity, and variation in key traits across individuals and their offspring (Stearns, 1976). Variations in the reproductive and survival abilities of individuals within a population have long been considered a key feature of life (Darwin, 1859) and are generally considered to be ubiquitous in natural populations (Bergeron et al., 2011; Kendall et al., 2011). Given the central role of life-history evolution in biology (Prasad & Joshi, 2003), both theorists and empiricists have been especially interested in the evolutionary consequences of variation in, and covariation between, life-history traits (e.g. Hastings & Caswell, 1979; Orzack & Tuljapurkar, 1989; Schaffer, 1974; Tuljapurkar et al., 2009). At the same time, ecologists have used analyses of variation in vital rates to learn how organisms respond to environmental change (e.g. Cooch et al., 2001; Garrott et al., 2003; Reid et al., 2004, 2022). Knowledge of how a population's vital rates vary among individuals and respond to changes in intrinsic and extrinsic conditions is becoming more important because rapid changes to Earth's climate are occurring and expected to continue and to affect populations of wild species across the planet (Gutt et al., 2021; Intergovernmental Panel on Climate Change, 2014; Petchey et al., 2015).

Long-term studies that monitor the development and life histories for large numbers of individually recognizable animals are valuable for learning about age-related variation in vital rates (Clutton-Brock & Sheldon, 2010). Data from such studies also allows researchers to assess how age-related changes in vital rates vary among individuals that differ in phenotypic traits and how such patterns vary with environmental conditions. In longitudinal studies of individuals, it is possible to connect events at various life stages to one another, which can be valuable for gaining insights about variation in survival and reproduction over an animal's lifespan. For example, reproduction in a given year might influence survival and/or reproduction in a subsequent year. Further, features of an individual's birth-cohort such as population density, environmental conditions can have long-lasting effects on the individual's life-history outcomes. Individual heterogeneity can also arise because individuals differ genetically and receive different maternal effects (Forsythe et al., 2021). Recently, results from studies of high-quality data from long-term monitoring of known-aged individual animals have provided valuable information for a variety of key questions regarding variation in vital

rates in wild populations and life-history trade-offs (Clutton-Brock & Sheldon, 2010; Festa-Bianchet et al., 2017). As nicely exemplified in several recent reviews, such studies have provided important insights regarding fitness costs of reproduction (Festa-Bianchet et al., 2019) as well as accumulating evidence for senescence in wild animals (Lemaître et al., 2015; Lemaître & Gaillard, 2017; Nussey et al., 2013). Important advances in understanding changes in survival and reproductive performance have come as recent developments in statistical methods for evaluating within- and between-individual variation in vital-rates have been applied to data from long-term, individual-based field studies (e.g. Cam et al., 2002; Rebke et al., 2010; van de Pol & Verhulst, 2006). Continued improvements in statistical methods for estimating diverse forms of individual heterogeneity in vital rates from capture-mark-recapture (CMR) studies with imperfect detection are especially valuable to life-history studies given that many field studies collect data using CMR methods (e.g. Gimenez et al., 2018; Kéry & Schaub, 2012; Link & Barker, 2010; Péron et al., 2010; Turek et al., 2016; Williams et al., 2002).

Here, I review how the long-term population study of Weddell seals in Erebus Bay, Antarctica has provided information on patterns, sources, and consequences of variation in age-specific vital rates and contributed to diverse aspects of the literature on life-history evolution. This southern-most population of breeding mammal has been the subject of an on-going CMR research program since 1968 (Siniff et al., 1977; Stirling, 1969a), and core aspects of the CMR protocols have been consistently applied since 1978 (e.g. Cameron & Siniff, 2004; Hadley et al., 2006; Paterson et al., 2018; Rotella et al., 2012). The philopatric nature of females and high detectability of seals (especially mother-pup pairs) when they are hauled out on the sea ice, has allowed the Erebus Bay Weddell seal population study to collect detailed data on survival and reproductive histories for large samples of individually marked seals. Over the past 20 years, a series of analyses has been conducted on data collected since 1978 from thousands of known-age animals to address questions about individual variation in reproduction and survival. Here, I provide information on the key attributes of the species and the study area, the historical context of the study and key players in the long-term demographic studies, the key questions and scientific advances made regarding variation in female vital rates over the past 20 years, unanswered questions and how they might be addressed in the future, and key challenges faced when working in the study system.

2 | KEY WEDDELL SEAL POPULATION ECOLOGY ATTRIBUTES

The Weddell seal is earth's southernmost living mammal with a circumpolar distribution around the Antarctic continent, where it is primarily associated with fast ice (Stirling, 1969a). Details of the species' life history have been described by numerous demographic studies conducted from the early 1900s to present (e.g. Chambert et al., 2015; Hadley et al., 2006; Hastings et al., 1999; Lindsey, 1937; Mansfield, 1958; Paterson et al., 2018; Proffitt et al., 2010; Rotella et al., 2012; Siniff, 1981; Siniff et al., 1977; Stauffer et al., 2013; Stirling, 1969a; Testa, 1994; Testa & Siniff, 1987; Wilson, 1907). In addition, many studies of Weddell seal physiology have been conducted as exemplified by an early book on the topic (Kooyman, 1981) and summarized in a recent review (Shero & Burns, 2022). Given the wealth of information available on the species, here I only provide a brief review of key attributes of the species life history that are pertinent to the Erebus Bay Weddell seal population studies.

Weddell seals have been studied in numerous areas (e.g. Lake et al., 2006; Mansfield, 1958; Stirling, 1969a) as they are the most accessible of the Antarctic seals species and are amenable to data collection when they form pupping colonies in Austral spring along cracks in the fast ice. The Weddell seal population in Erebus Bay located at the southern end of McMurdo Sound in the southwestern Ross Sea (−77.62° to −77.87°S, 166.3° to 167.0°E) is the world's largest aggregation site (LaRue et al., 2021) and has been intensively investigated since the 1960s, which has been possible because of its proximity to United States (McMurdo Station) and New Zealand (Scott Base) research stations (Figure 1).

Females aggregate near cracks in the sea ice and give birth from mid-October through mid-November to ~400–600 pups each year at 8–14 colonies (Figures 1 and 2). A mother typically gives birth to a single pup weighing ~30kg, is the sole provider of parental care, and relies heavily on stored body reserves while nursing a pup for 4–6 weeks during which time a pup typically gains ~70kg and a mother loses ~33% of her body mass (Macdonald et al., 2020; Paterson et al., 2016; Wheatley et al., 2006, 2008). During lactation, mother-pup pairs are closely associated and readily identified as a pair. Pups begin to enter the water at 8–10 days of age and swim with their mothers, who abrade the sea ice with their teeth to maintain holes in the sea ice (Stirling, 1969a). Males maintain underwater territories beneath the ice of pupping colonies and polygynous mating occurs underwater near the end of weaning (Cline et al., 1971; Harcourt et al., 2007; Siniff et al., 1977). Yearling and 2-year-olds are rarely observed in the colonies but older pre-breeders and females that are on sabbatical from pupping regularly attend pupping colonies. Mothers show strong fidelity to the study area for giving birth, which they typically begin to do when 7 or 8 years old and do 2 out of every 3 years thereafter. Seals of both sexes display strong fidelity to the study area once they are several years old (Stauffer et al., 2013; Stirling, 1969a). Weddell seals have no above-ice predators, are readily approached (Wilson, 1907), and can live to 32 years

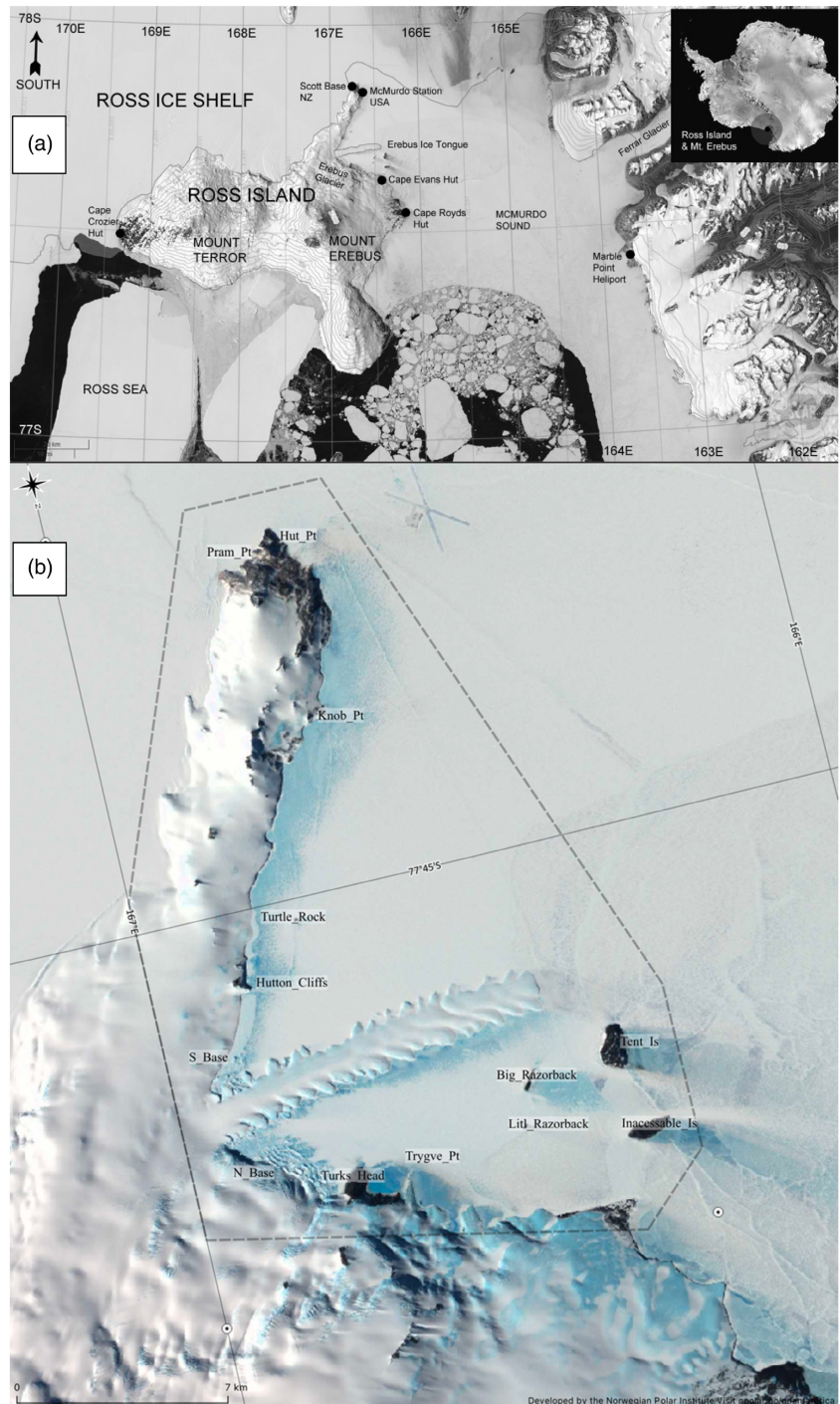
of age. Thus, individuals can be marked and re-encountered many times if they survive the early years of life.

The Erebus Bay population is ideal for studying variation in vital rates as it is located near a large research station and has been studied during each pupping season for multiple decades. As a result, high-quality CMR data exist for many thousands of known-age females with known reproductive histories across diverse environmental conditions. However, several realities of the study system are worth noting. First, the proximity of the seal colonies to two research stations led to Weddell seals being harvested to feed dog teams from 1956 through 1984 with at least 350 seals killed in 1956 and lesser numbers (50–100 adults) per year thereafter (Crawley, 1978; Stirling, 1971; Testa & Siniff, 1987). Based on analyses of diverse demographic characteristics, Stirling (1971) reported that the population initially declined, then rapidly expanded, and subsequently stabilized in response to the harvests. Pup production levels in the ensuing decades were indeed remarkably stable at ~420 births per year (Chambert et al., 2012). Weddell seals are now afforded protection through the Antarctic Treaty and Antarctic Conservation Act, national laws such as the U.S. Marine Mammal Protection Act, and the world's largest Marine Protected Area (MPA) that was established in 2015 in the Ross Sea region (Brooks et al., 2021). Almost 80% of the Ross Sea region MPA (2.09 million km²) is closed to commercial fishing, but limited commercial fishing for Antarctic toothfish *Disostichus mawsoni*, a species that Weddell seals eat and compete with for prey, began in the late 1990s and is allowed in some portions of the MPA, which could affect seal population dynamics (Ainley et al., 2021; Ainley & Siniff, 2009; Salas et al., 2017). It is also important to note that the remoteness and climate of the high-latitude area present challenges to investigating sources of variation in vital rates. Although field observations are readily obtained in October through mid-December, sea-conditions deteriorate soon after weaning occurs in December such that travel on the sea ice is typically unsafe and not allowed other than at select near-shore haul-out sites used by moulting seals in late-January and February (Shero & Burns, 2022). Winter work on Weddell seals has been rarely done due to logistical challenges of work at the high-latitude site, which have precluded almost all winter field work (though movement data can be collected via telemetry). Data on Weddell seal predators and prey are quite limited given the nature of the region, which has led to the use of environmental proxies, for example sea-ice extent, rather than direct measures of food and predators. Thus, detailed information on movements of most individuals is lacking, most mortality events go undetected, and much remains to be learned about when and where critical resources are acquired.

3 | BRIEF HISTORY OF THE EREBUS BAY WEDDELL SEAL POPULATION STUDY

Wilson (1907) observed Weddell seals in Erebus Bay during a British expedition to the region during 1901–04 and described the timing of key life events and behaviour through the annual cycle. Studies

FIGURE 1 Erebus Bay study area: (a) location relative to the Antarctic continent (inset) and Ross Island (SCAR Antarctic Digital Database; <https://www.coolantarctica.com/schools/Antarctica-maps-ross-island.php>); (b) study area boundary (grey dashed lines) and named locations of major pupping colonies and seal aggregations (produced with Quantarctica—<https://www.npolar.no/quantarctica/>, LIMA high-resolution imagery [15 m]).



of Weddell seal population dynamics began in the 1960s with work by researchers from New Zealand (Smith, 1966; Stirling, 1969a, 1971) and the United States (Siniff et al., 1977). Since 1973, the tagging program initiated in 1971 by Donald Siniff, University of Minnesota, has included multiple, systematic surveys of marked and unmarked Weddell seals in the Erebus Bay study area, which along with annual efforts to outfit large numbers of seals with uniquely numbered tags has provided the core data for many CMR studies on seal abundance and vital rates from 1977 to present. The studies have been funded by the National Science Foundation (NSF) of the United States through a series of grants for short-term

research projects to Siniff (1976–1988, with A. Erickson in 1976–1977); Michael Castellini and J. Ward Testa (1989–1992); Siniff (1993–2001); Robert Garrott, Jay Rotella, and Siniff (2002–2021); and Rotella (2022–2026). At the end of the 2021 field season, the project's database contained information for 306,916 encounters of 27,978 uniquely marked individuals.

Several key aspects of the project have remained consistent: study area boundaries, annual marking of pups and adults, and a systematic set of CMR surveys of all marked and unmarked individuals. Several features have been improved or added as well. In early years, the project attempted to record annual pup production and

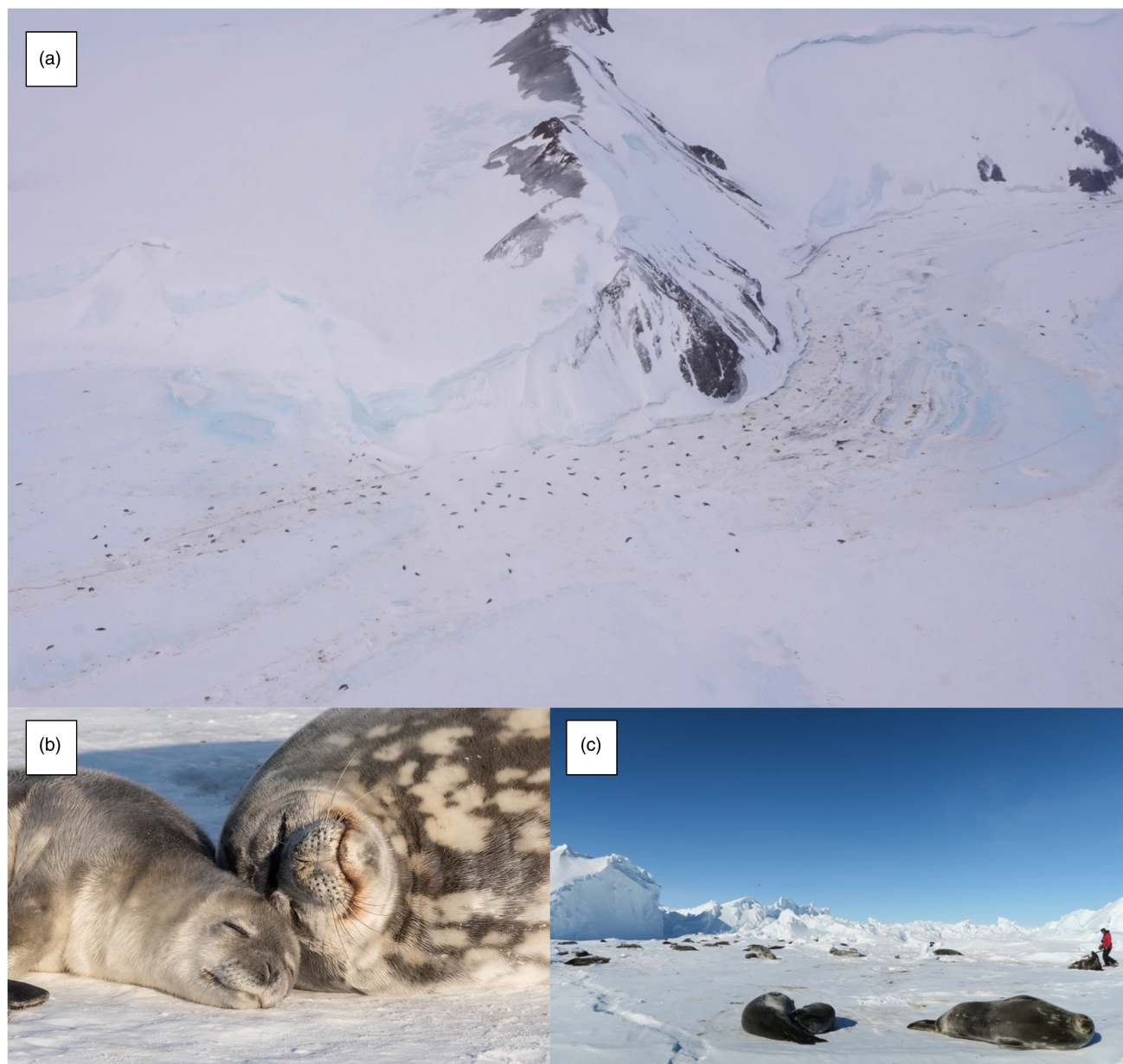


FIGURE 2 Examples of Weddell seals in Erebus Bay, Antarctica: (a) the largest Erebus Bay colony at Hutton Cliffs in Erebus bay, (b) a mother-pup pair, and (c) R.A. Garrott checking mother-pup pairs at North Base colony. Photos: (a and c), Jay Rotella, (b) William Link.

to individually mark a sample of pups and adults each year. From 1982 to present, virtually every pup born in the study area has been tagged each year. In recent decades, the project has continued to tag a sample of untagged males each year, and efforts have been made to tag every adult female. Tag retention rates, which are used to correct survival rate estimates for tag loss, improved after 1982 (range: 0.95–0.999/year) as better tags were used and greater efforts were made to replace tag sets showing signs of wear or damage (Cameron & Siniff, 2004). Over the past 20 years, through efforts led by Garrott, the project added information on body mass dynamics for a sizeable sample of mothers and pups (Macdonald et al., 2020; Paterson et al., 2016). The project has been made possible by the support of the United States Antarctic Program, support contractors

associated with the Program, and the daily field work of many graduate students and research technicians.

4 | VARIATION IN WEDDELL SEAL VITAL RATES

In recent decades, many animal population studies have shifted their primary focus from direct study of the state variable of population size to study of the vital rates (birth, death, immigration, and emigration) that are responsible for changes in population size, and inferences about such changes have been valuable to evolutionary ecology and to basic and applied population ecology (Lebreton

et al., 2009). The Erebus Bay Weddell seal population study has undergone a similar shift as the project's CMR database has grown to include many more individuals, ages, and years over a period when the available methods for analysis of vital rates have improved to allow much greater flexibility in the sources of variability that can be accommodated. Below, I summarize key developments that have been made with respect to vital-rate variation for females and organize the review around several core topics: (1) early-life survival and age at first reproduction, (2) costs of reproduction to survival and future reproduction, (3) temporal process variation in vital rates and the demographic buffering hypothesis, and (4) survival and reproductive senescence.

4.1 | Early-life survival and age at first reproduction

In long-lived species, juvenile survival is often lower and more variable than adult survival, and temporal variation in juvenile survival rates may be responsible for much of the realized variation in population growth rate (λ) (Eberhardt, 2002; Eberhardt & Siniff, 1977; Gaillard et al., 1998, 2000). Given the potential importance of juvenile survival and the many thousands of Weddell seal pups that have been tagged and monitored annually in Erebus Bay, multiple studies of juvenile survival have been conducted, with the earliest conducted in the late 1990s and early 2000s (Cameron & Siniff, 2004; Hastings et al., 1999; Hastings & Testa, 1998; Testa, 1987a). Hastings et al. (1999) reported that annual survival rates were much lower in the first 2 years of life (~0.5–0.6) than at subsequent ages (~0.93) and identified sources of variation that helped stimulate subsequent work on relationships between early-life survival and features of an individual's mother and the conditions experienced early in life.

Over the past 20 years, research on early-life survival has continued and often been part of broader work that also addressed questions about recruitment and age of first reproduction. For many long-lived species with delayed reproduction, life-history trade-offs between current and future reproduction may exist (Gadgil & Bossert, 1970; Roff, 1992), which can lead to considerable individual variation in the age of first reproduction (Harvey & Zammuto, 1985) as well as fitness and lifetime reproductive output (Stearns, 1976, 1992). Hadley et al. (2006) took advantage of multi-state mark-recapture models (Arnason, 1972, 1973; Brownie et al., 1993; Hestbeck et al., 1991; Lebreton et al., 2009; Schwarz et al., 1993), the strong site fidelity of Weddell seal mothers, and the fact that both non-reproductive and pup-producing females are observable in pupping colonies to present a novel approach for estimating survival rates for pre-breeders and age-specific probabilities of recruitment to the pup-producing portion of the population. The work provided the first formal estimates of age-specific probabilities of recruitment. Age at first reproduction varied widely among individuals (range: 4–14 years of age, mean = 7.6, SD = 1.7). Results affirmed predictions from life-history theory that age at

first reproduction should be sensitive to environmental variation (Eberhardt & Siniff, 1977; Goodman, 1981) and led to future investigations of individual variation in female reproductive output and the fates of their offspring.

A follow-up study was conducted to evaluate various hypotheses regarding how offspring survival and recruitment probabilities vary as functions of maternal characteristics (including age at first reproduction, maternal age and reproductive experience). Results provided evidence of contrasting influences of maternal age on survival and recruitment rates of their offspring. Specifically, survival increased with maternal age, whereas recruitment probabilities were highest for seals born to young mothers, which is suggestive of countervailing selection at different life stages (Pemberton et al., 1991; Price, 1984). Hadley et al. (2007b) speculated that females that begin reproduction at young ages are likely higher-quality females that are also likely to be of smaller size than older mothers when they produce their first pups, such that a pup born to a young mother tends to wean at a lower weight with poor early-life survival prospects. However, if such a pup survives early life, it may display the high-quality traits of its mother and have an above-average probability of recruiting.

At the time that research on the project was identifying important relationships between a mother's age and her offspring's survival and recruitment probabilities, work on body mass dynamics reported that there is substantial age-related variation in maternal body mass at parturition that could explain why offspring survival might increase with maternal age (Proffitt et al., 2007). Specifically, the research found that maternal body mass at parturition increases with age through the teens before showing senescent declines and that females with higher body mass are expected to transfer more energy to their pups during lactation, which could increase their survival prospects. A follow-up investigation found evidence of a positive relationship between body mass at weaning and juvenile survival but noted that results for female offspring were more equivocal (Proffitt et al., 2008). Subsequently, much more research has been conducted on body mass dynamics, and future investigations of relationships between offspring survival and maternal age should consider key results of that work. First, younger and older mothers do tend to weigh less at parturition than do prime-age mothers and indeed give birth to lighter pups (Paterson et al., 2016). However, consistent with terminal allocation (Weladji et al., 2010), older mothers allocate more of their declining resources to their offspring during lactation and wean pups that weigh a similar amount to those weaned by prime-aged mothers (Paterson et al., 2016). Such compensation might reduce the consequences of being born at a lighter birth mass but could also incur costs later in life (Marcil-Ferland et al., 2013; Metcalfe & Monaghan, 2007). Second, although maternal age is an important determinant of mass of mothers and their offspring, there is also a great deal of individual variation in mass among mothers of the same age (Macdonald et al., 2020; Paterson et al., 2016) such that multiple maternal features and environmental conditions will likely need to be considered in future efforts to assess sources of variation in offspring survival.

Hadley et al. (2007b) reported that oceanographic conditions were related to annual recruitment rates but not to early-life survival rates, which prompted a follow-up study to evaluate the duration of potential birth-year influences on survival rates and the importance of birth- and current-year influences on survival and recruitment rates (Stauffer et al., 2013). Results indicated that both birth- and current-year conditions are important to survival rates of pre-breeders and that conditions experienced at birth were of intermediate duration (6 years), which adds to the literature on persistent among-cohort differences in survival and reproduction (e.g. Gaillard et al., 1997; Monaghan, 2008; Reid et al., 2003; van de Pol et al., 2006). However, no relationships between recruitment rates and birth-year conditions were detected, which is perhaps not surprising given that proxies for prey availability and predator abundance, for example sea-ice extent, must be used in this ice-covered region.

4.2 | Costs of reproduction

Information on reproductive costs is valuable to life-history theory as the trade-offs between current reproduction and future survival and reproduction are hypothesized to affect the life-history strategies of many species (Roff, 1992; Stearns, 1992; Williams, 1966). Such costs in female Weddell seals have been of strong interest (Siniff, 1981; Testa, 1987b) and are expected as females expend a great deal of energy producing and caring for pups, which could decrease energy available for survival and subsequent reproduction (Wheatley et al., 2006). Accordingly, more complex multistate modelling was done to assess trade-offs at the phenotype level (Hadley et al., 2007a), which yielded results that indicated that reproduction imposes an immediate cost to survival: mean annual survival rates were lower for females that produced a pup than for those that did not (annual averages [and SE]: 0.91 [0.04] and 0.94 [0.03], respectively, which represents a 50% increase in mortality [0.09—breeders; 0.06—nonbreeders]). Costs of reproduction to future reproduction were only detected for first-time mothers: females that were primiparous in the previous year had a lower breeding probability (annual average for rate [and SE]: 0.46 [0.06]) than did females that were experienced mothers (0.67 [0.05]) or that skipped reproduction (0.67 [0.06]) in the previous year (Hadley et al., 2007a). The findings contrast with the 'prudent parent' strategy (Cam et al., 1998; Drent & Daan, 1980) and suggest that Weddell seal females endure costs of reproduction, which is more in keeping with a flexible strategy with occasional reproductive investments that come at a cost (e.g. Reid, 1987).

Given developments with hierarchical modelling that yielded important insights for other species (Cam et al., 2002), Chambert et al. (2013) re-evaluated reproductive costs in Weddell seal females using Bayesian multistate models that included a random effect of individual on probabilities of reproduction to analyse data from first reproduction through the last year each individual was known to have been alive. The updated analysis detected a substantial cost

of reproduction that was not found when latent heterogeneity was ignored. Specifically, an experienced mother was more likely to produce a pup if she had skipped reproducing the year before (average rate [95% Credible Interval]: 0.76 [0.70–0.81]) than if she had not (average rate [95% Credible Interval]: 0.67 [0.61–0.73]). The change in results occurred because frailer females are likely to skip reproduction more often, whereas more robust females are likely to produce pups more often such that females with different frailty levels provide more information about different types of transitions if heterogeneity is not considered.

A subsequent study (Paterson et al., 2018) analysed a more complete set of encounter histories, that is, not truncated at the year the female was last known to be alive, using more complex multi-state models that included individual heterogeneity in rates of survival and reproduction and split skip breeders into two states (attending colonies or not) to incorporate temporary emigration that is known to occur (Chambert et al., 2015; Stauffer et al., 2014). Findings supported the main results of prior analyses but also (a) detected a negative relationship between a female's age at first reproduction and her probability of reproduction, which supports suggestions from earlier work that females who recruit earlier in life are of higher quality (Hadley et al., 2007b), (b) estimated a much greater level of among-individual heterogeneity in reproduction, and (c) reported a negative correlation between individual random effects for survival and reproduction. Results from Chambert et al. (2013) and Paterson et al. (2018) lend further support to conclusions of previous studies that noted the importance of accounting for individual heterogeneity in studies of life-history trade-offs (e.g. Van Noordwijk & Dejong, 1986; Vaupel & Yashin, 1985; Weladji et al., 2008). Analysis of the correlation between reproductive rates of mothers and their female offspring provided evidence that reproductive rates might be weakly heritable (Chambert et al., 2014).

4.3 | Annual variation in vital rates and the demographic buffering hypothesis

Knowledge of how different age- and stage-specific vital rates vary temporally is key to understanding life-history evolution in stochastic environments and to predicting how populations will respond to changing environmental conditions (Hilde et al., 2020). The demographic buffering hypothesis (Gaillard et al., 2000; Gaillard & Yoccoz, 2003; Hilde et al., 2020; Morris & Doak, 2004; Pfister, 1998) predicts that life histories should evolve to buffer vital rates that are most important to fitness from temporal environmental variation, which should typically lead to environmental variation having the least impact on adult survival and greater impacts on reproduction and survival of younger animals in long-lived species (e.g. Gaillard et al., 1998, 2000; Jenouvrier et al., 2003; Reid et al., 2004). Research conducted on Weddell seal vital rates through 2006 suggested that survival of juveniles had higher temporal variation than rates for adults (Cameron & Siniff, 2004; Hadley et al., 2006; Hastings et al., 1999; Testa, 1987a), which provided preliminary

evidence of demographic buffering and prompted the first formal evaluation (Rotella et al., 2012) and two important associated efforts (Chambert et al., 2012; Paterson et al., 2018).

The formal evaluation was done with a multi-step approach that (i) simultaneously estimated annual rates of survival, recruitment, and reproduction that were age- and state-specific, where states refer to a female's reproductive status in the previous year, using 30 years of CMR data and multistate CMR models (Hadley et al., 2006, 2007a), (ii) estimated mean vital rates and the process variance–covariance of the rates using recent advances in hierarchical modelling and Bayesian methods, (iii) estimated λ 's sensitivity to vital rate changes by constructing and analysing a matrix model for the population, and (iv) compared estimated process variation with sensitivity values (Rotella et al., 2012). The results provided strong evidence of demographic buffering as temporal process variation was lowest in the vital rates to which λ was most sensitive (adult survival rates) and greatest in the vital rates to which λ was least sensitive (probabilities of recruitment and reproduction). Additional support for demographic buffering came from a subsequent analysis of how the population's vital rates changed during 2001–2005 (Chambert et al., 2012) when the largest iceberg ever recorded from Antarctica (295 km long, 40 km wide) calved from the Ross Ice Shelf and strongly disturbed the Ross Sea ecosystem (Arrigo et al., 2002; Kooyman et al., 2007; Seibel & Dierssen, 2003). During the iceberg event, recruitment and reproduction were greatly reduced, but adult survival rates changed little. Adult females employed a flexible

reproductive strategy to reduce reproductive effort and maintain high survival rates during the iceberg period, which allowed the population to quickly return from the lowest level of pup production ever documented to levels at or above the long-term average immediately after the iceberg event ended.

A subsequent evaluation of demographic buffering in vital rates for recruited females (Paterson et al., 2018) improved on several key aspects of previous analyses. In particular, the hierarchical analysis incorporated individual heterogeneity in rates of survival and reproduction, added age-structure to state-specific survival rates of recruited females, and allowed skip breeders to temporarily emigrate. The results confirmed earlier findings that annual variation in adult survival is low relative to variation in reproductive rates and revealed that rates of temporary emigration are typically low but occasionally increase during challenging environmental conditions (Figure 3). The highest rate of temporary emigration occurred in the middle of the iceberg period, which suggests that skip breeders also employ a flexible colony-attendance strategy as part of their flexible reproductive strategy. Given that, future investigations of environmental covariates that might be associated with annual variation in temporary emigration seem warranted as such variation affects local abundance and pup production. Investigations of environmental drivers of annual variation in rates of reproduction are also warranted as multiple analyses have reported notable levels of temporal process variation in reproductive rates.

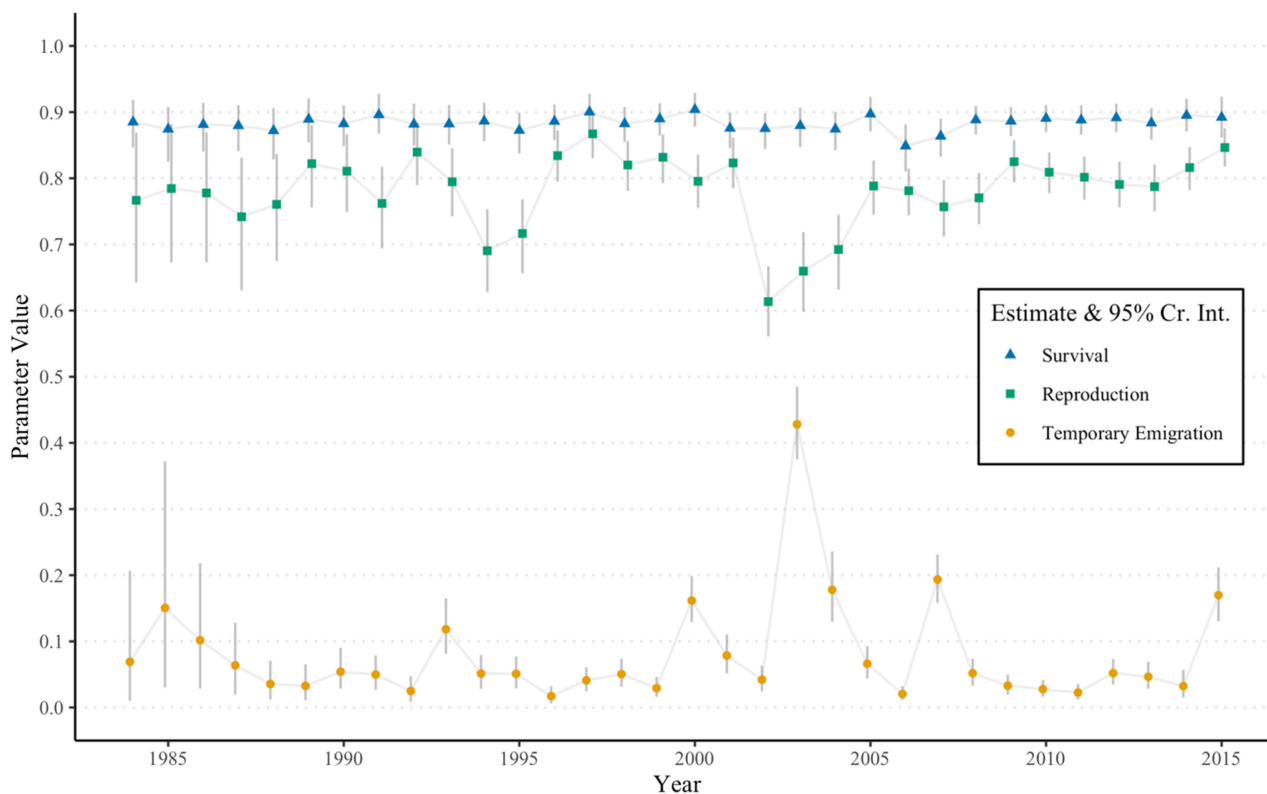


FIGURE 3 Estimated annual probabilities of survival, reproduction, and temporary emigration for a typical Weddell seal female that was a 12-year-old experienced mother that first reproduced at 7 years of age.

4.4 | Senescence in vital rates

Ecologists and evolutionary biologists have long been interested in understanding the diversity of patterns that exist for senescence, that is, “the decline in age-specific contributions to fitness with increasing age” (Gaillard & Lemaître, 2020, p. 4). A core set of evolutionary theories of aging hypotheses provides a solid theoretical framework (Hamilton, 1966; Kirkwood, 1977; Medawar, 1952; Williams, 1957) and, in recent decades, long-term, individual-based studies of wild animals have provided important evidence for demographic senescence, age-related declines in rates of survival and reproduction, as well as in physiological function (Gaillard & Lemaître, 2020; Monaghan et al., 2008; Nussey et al., 2013). Initial attempts at detecting age-related survival variation in Weddell seals identified early-life improvements but failed to detect late-life declines (Cameron & Siniff, 2004; Hastings et al., 1999). The authors acknowledged that the datasets available at the time contained limited or no information for individuals beyond their late teens, and continued monitoring has revealed that females can live to 32 years of age (current maximum lifespan observed). More recent studies of demographic senescence in the Erebus Bay Weddell seal population analysed data for thousands of recruited females that includes records from multiple birth cohorts that have been monitored for ≥ 25 years (Chambert et al., 2013; Paterson et al., 2018). Recruited females are highly detectable, and, given their high survival rates and low rates of temporary emigration (see above), each typically provides CMR data for multiple years that includes annual reproductive state, which is ideal for assessing demographic senescence. As described above, the more recent studies (Chambert et al., 2013; Paterson et al., 2018) also incorporated numerous advances in hierarchical modelling for CMR data that allowed them to assess age-related changes in vital rates while also accounting for variation associated with reproductive state and possible individual variation in vital rates and contribute important information to the rapidly growing body of literature on demographic senescence in vertebrates.

Chambert et al. (2013) investigated age-related changes in a female's probability of reproduction using information on annual reproductive states beginning when an individual first reproduced and ending when an individual was last seen alive; the results provided the first evidence that the probability of reproduction increased to a peak when females were in their mid-teens and then declined. Such results provided valuable information on age-related changes in reproduction in non-humans, a topic in need of greater attention at the time (Monaghan et al., 2008). In a logical extension to that work, Paterson et al. (2018) estimated age-related changes in both survival and reproductive rates by evaluating competing models that combined different functional forms of age for each vital rate and included/excluded individual random effects. Results indicated distinct differences in age-related changes in the two vital rates. Whereas probabilities of reproduction increased from primiparity to age 16 and then declined, the probability of survival steadily declined after the onset of reproduction (Figure 4). The co-occurrence of increasing reproductive rates and declining survival rates early

in reproductive life provides strong evidence that trade-offs between reproduction and survival change as age-specific realized reproductive values change. For females older than ~16 years of age, simultaneous age-related declines in both vital rates suggest that reproductive performance in older animals is governed by a decline in physiological function. Previous work on Weddell seals has found that upper canine and incisor teeth used to abrade ice and maintain breathing holes show marked wear as seals age, which may increase risk of mortality (Stirling, 1969b), and demonstrated muscular senescence, which could be associated with reduced foraging efficiency (Hindle et al., 2009). However, it is not known if females who invest more energy to reproduction incur more rapid physiological declines, which could occur because mothers actively abrade the ice around breathing holes to make it easier for pups to exit the water and because mothers undergo rapid weight loss while nursing pups. It would be useful for future work to assess to what extent if any, such aging mechanisms are affected by reproductive bouts versus inherent to the physiological nature of Weddell seals (Cohen et al., 2020). Assessments of cumulative costs of reproduction and their possible role in demographic senescence are needed (Festa-Bianchet et al., 2019; Kroeger et al., 2018b).

5 | CONCLUSIONS

Over the past 20 years, through a series of inter-related studies of long-term data, details of the flexible reproductive strategy employed by the species have been revealed and diverse sources of variation in vital rates of female Weddell seals have been identified, which has contributed valuable information about the species and to the literature on life-history evolution that comes from other long-term studies. The results add information on vital-rate variation in Antarctic species (e.g. Barbraud & Weimerskirch, 2001; Jenouvrier et al., 2018) and allow for comparisons in such variation for Weddell seal populations in other regions of Antarctica (Lake et al., 2008). Results for Weddell seals also contribute to the modest number of long-term studies of vital-rate variation in pinnipeds, which are exemplified by, but not limited to, work on southern elephant seals *Mirounga leonina* (e.g. Oosthuizen et al., 2019; Pistorius et al., 2011) and grey seals *Halichoerus grypus* (e.g. Bowen et al., 2006). Results from marine systems contribute to the broader set of long-term studies of vital-rate variation, which tends to be dominated by work in terrestrial ecosystems (e.g. Clutton-Brock & Sheldon, 2010; Festa-Bianchet et al., 2017). Understanding of vital-rate variation, life-history evolution, and demographic responses to changes in environmental conditions will continue to improve if studies of marked individuals from a diverse range of taxa and ecosystems can continue to provide detailed demographic data,

For Weddell seals, key findings regarding variation in age-specific vital rates are as follows. Annual survival rates are relatively low early in life (~0.5 for pups and yearlings) such that only ~20% of females in a birth cohort survive and reproduce. Environmental conditions as well as the features of a pup's mother such as her age,

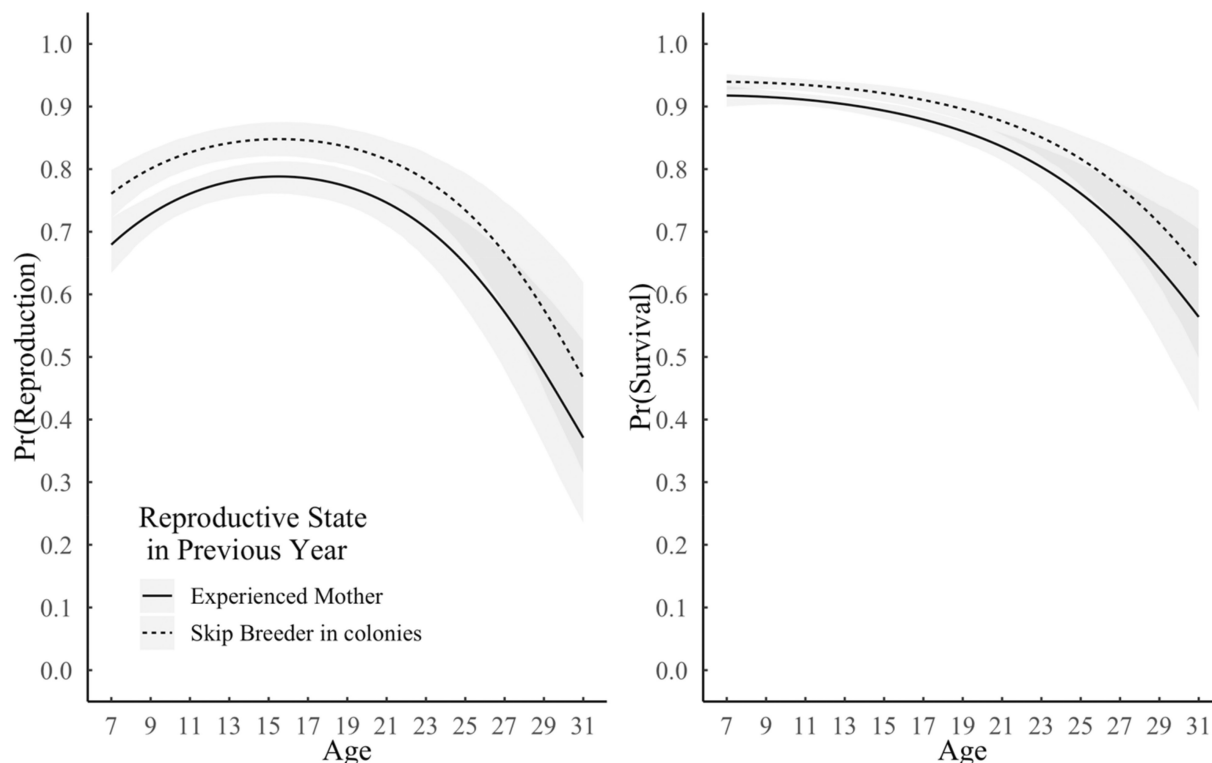


FIGURE 4 Age- and breeding-state-specific estimates of the probabilities of reproduction and survival in a typical year for a female Weddell seal that first produced a pup at age 7 years old (ages are in years; breeding states refer to the female's breeding state in the previous year).

age at first reproduction and reproductive experience combine to influence a newborn's survival prospects. Although pups with prime-aged mothers that recruited at a young age have better demographic prospects than other newborns, luck likely plays a prominent role relative to trait variation and affects which pups go on to produce offspring of their own (Snyder et al., 2021; Snyder & Ellner, 2018, 2022).

Age at first reproduction varies from 4 to 14 years of age (average = 7.6) and occurs when females are still growing larger and heavier, which may help explain why first-time mothers suffer costs of reproduction to subsequent survival and reproduction. Recruitment rates also vary by year, which further suggests that luck likely plays at least some role in when females begin reproducing. After recruiting, a female's probabilities of reproduction vary by year and age, recent reproductive state, and identity. Bouts of reproduction in which female's rely heavily on stored body reserves and lose ~33% of their body mass during lactation impose costs to survival and reproduction in the subsequent year.

Trait variation among females leads expected lifetime reproductive output to vary by 4–6 pups among females with different latent and observed characteristics. Luck plays a further role as realized reproductive output among females that recruited has ranged from 1 to 18 pups (mean = 6) over the first 25 years of life. Although females do not appear to be able to avoid small, but non-trivial, costs of reproduction to survival, demographic buffering of fitness from environmental variation appears to be a key aspect of the species'

flexible reproductive strategy as temporal variation is lowest for adult survival rate, to which asymptotic population growth rate is most sensitive, and greatest in breeding probabilities, to which asymptotic population growth rate is least sensitive.

Females peak in terms of body mass and probability of reproduction in their teens before experiencing senescent declines in both attributes. Survival rates also show senescent declines but follow a different pattern with rates steadily declining after the onset of reproduction. Through the combination of luck and individual traits including age, reproductive history, individual identity, environmental conditions faced each year, lifespans and lifetime reproductive output vary greatly among individuals. Most females (~80%) live just a few years or less and produce no offspring, whereas the most highly productive individual gave birth to 23 pups in a 31-year lifespan. As the project goes forward, it should be possible to expand on the work done to date as additional years of data that are collected for more individuals born to mothers of known age and with known reproductive histories over a wider variety of environmental and demographic conditions are analysed with ever-improving analytical tools for CMR data and for obtaining remotely sensed environmental data.

6 | NEXT STEPS

Now that the long-term research has identified and quantified diverse sources of variation in vital rates, logical next steps are

to learn more about the processes that lead to variation, further refine our understanding of the patterns of vital-rate variation, consider how trait variation combines with luck to influence individual variation in lifetime reproductive success, evaluate the consequences of individual variation in traits to individual demographic outcomes and to population growth, and develop predictions of population responses to possible future environmental conditions. Results from the past decade provide an opportunity to improve understanding of drivers of an individual's early-life survival and recruitment prospects. Pups vary strongly in terms of their birth timing (Rotella et al., 2016), body mass at birth and late in lactation (Macdonald et al., 2020; Paterson et al., 2016), the amount of time they spend in the water during lactation (Petch et al., 2022), and the environmental conditions they experience early in life (Stauffer et al., 2013, 2014). Thus, it would be valuable to evaluate the importance of phenotypic variation resulting from variation in maternal effects, behavioural traits, and environmental conditions on early-life survival and recruitment probabilities. Such research would contribute to the modest number of studies on transgenerational effects on individual vital rates (Gaillard & Lemaître, 2020).

A better understanding of environmental drivers of annual variation in Weddell seal vital rates is needed but may be challenging to achieve given the limited information available for predators and prey in the study system. Regardless, efforts to better understand relationships between vital rate variation and environmental conditions and changes in toothfish populations associated with commercial fishing are warranted (Ainley et al., 2021; Salas et al., 2017) and ideally would include data for penguins and assess community-level responses. Based on increases in annual pup production over the past 15 years, it appears that the population has grown after decades of stability. Thus, it might be possible in the near future to also investigate possible density dependence in vital rates (Fowler, 1981).

Future work on costs of reproduction should consider whether costs are context dependent (Festa-Bianchet et al., 2019; Gaillard et al., 1998), and if so, to identify key covariates. Our sole investigation of temporal changes in costs of reproduction (Chambert et al., 2013), which provided marginal evidence of context dependence, relied on a mega-iceberg event of relatively short-term duration when comparing costs in different environmental conditions. In the future, context dependence can be re-evaluated with an additional decade or more of data for a longer period of contrasted environments. It would also be useful to evaluate cumulative costs of reproduction and possible effects of long-term reproductive history on current reproduction and survival (Kroeger et al., 2018a). Finally, analyses of repeated measures of maternal mass at parturition and during lactation across females with contrasting reproductive histories could be conducted to assess possible somatic costs of reproduction (Festa-Bianchet et al., 2019).

Our recent investigations of vital rates have found notable levels of individual heterogeneity in vital rates (Paterson et al., 2018).

Improvements in our understanding of factors influencing on the origins of individual variation in vital rates could benefit from combining demographic work with behavioural and physiology investigations of individuals (e.g. Gangloff et al., 2018), which should be possible given the strong history of physiology studies on Weddell seals (Shero & Burns, 2022), recent work on the Weddell seal genome that links physiological traits to genetics (Noh et al., 2022), and improved ability to track movements of marine predators in the Southern Ocean (Hindell et al., 2020). Future investigations of individual heterogeneity should also evaluate the possibility that individual heterogeneity is dynamic rather than static throughout life (Tuljapurkar et al., 2009).

Future analyses should quantify the degree to which individual variation in life-history outcomes is determined by individual traits, environmental conditions, and random chance by applying recent analytical developments to existing demographic data (Snyder & Ellner, 2022) and taking advantage of recent advances in integral projection modelling (Ellner et al., 2016; Ellner & Rees, 2006) that allow character states to be continuous traits such as body mass and/or individual heterogeneity in vital rates.

Recent developments in vital-rate modelling provide opportunities to re-evaluate patterns of demographic senescence. It would be valuable to compare support for models that use linear, quadratic, or logarithmic functions of age, which have been used in our recent analyses, with alternatives that use splines (Dahlgren et al., 2011) or thresholds (Berman et al., 2009) for modelling relationships between age and vital rates. As well, it would be instructive to compare results from approaches that incorporate individual heterogeneity using random effects (Cam et al., 2002; Paterson et al., 2018) with those that employ finite mixtures (Hamel et al., 2017; Jenouvrier et al., 2018; Péron et al., 2010).

Finally, it would be valuable to develop a population model for Weddell seals that uses estimated vital rates to generate reliable predictions of how the population's size, composition, and demographic vital rates are expected to vary in response to changes in, and possible interactions between, extrinsic (environment) and intrinsic (population attributes) conditions. Such predictions would be valuable for the Erebus Bay population of Weddell seals given that unprecedented reductions in sea-ice extent occurred in recent years (Parkinson, 2019) and the development of a commercial fishery in the region, which could affect food availability for seals (Ainley & Siniff, 2009; Blight et al., 2010; Salas et al., 2017).

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AUTHORS' CONTRIBUTION

J.J.R. wrote the manuscript, performed revisions and prepared the figures.

CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

This paper is a synthesis of previous publications and does not use new data.

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