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RESEARCH ARTICLE

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Drivers of age at first reproduction in the wandering albatross (*Diomedea exulans*): Demographic factors, environmental conditions and sex-specific responses

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Abstract

1. Age at first reproduction is an important life-history trait that marks the beginning of reproductive allocation in long-lived organisms and drives patterns of life-history strategies. Demographic factors and environmental conditions likely affect age at first reproduction through multiple pathways: food resources availability and energy storage from birth to recruitment, competition for breeding sites and mate availability.
2. Using a unique 35-year dataset of individual-based mark–recapture data from a wandering albatross (*Diomedea exulans*) population at Crozet (southern Indian Ocean), we investigated how demographic factors and environment influence age at first reproduction. The population experienced major fluctuations, declining by 50% in the 1970s before partially recovering in the 1980s. It was also exposed to important environmental changes, including variations in large-scale climate phenomena and changes in subtropical anticyclone systems like the Mascarene high pressure system.
3. We used multi-event hidden Markov models to estimate age-specific survival and breeding probabilities for each sex separately. From these models, we estimated the age at first reproduction through absorbing Markov chains while accounting for imperfect detection. We investigated how demographic factors (population density at birth and mate availability at recruitment) and environmental conditions (at birth and recruitment) influenced age at first reproduction through their effects on survival and breeding probabilities.
4. Age at first reproduction declined across cohorts for both sexes from 1970 to the mid-1980s, then stabilized. Females recruited at 9.0 years in early cohorts versus 7.5 years in later ones; males declined from 10.2 to 9.2 years. Environmental

conditions at birth, particularly the El Niño Southern Oscillation and the Mascarene high, influenced recruitment timing through delayed effects of natal condition on breeding probability rather than survival. Mate availability strongly facilitated earlier recruitment in both sexes, while natal population density delayed male recruitment specifically.

5. Recruitment timing in wandering albatrosses is shaped primarily by developmental programming during the natal period rather than by immediate environmental triggers at sexual maturity, with mate availability and population density modulating these early-life effects in sex-specific ways. Given that recruitment is an important life-history event linked to population-level reproductive rates, accurate demographic projections require models accounting for cohort-specific effects under changing environments.

KEYWORDS
demography, hidden Markov model, life history, recruitment, reproductive biology, seabirds

1 | INTRODUCTION

Age at first reproduction, or recruitment, marks an important transition in an organism's life (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009) and is a core trait in life-history theory (Stearns, 1992). Since Cole (1954) seminal work on reproductive strategies, the timing of first reproduction has been recognized as central to a fundamental trade-off in life histories: balancing the benefits of early reproduction against the costs of reduced survival or future reproductive success (Roff, 1993; Stearns, 1992). This trait determines not only when individuals begin contributing to population growth, but also influences the entire trajectory of their reproductive life (Stearns, 1992). Early breeding can maximize lifetime reproductive success, but high investment in early reproduction may compromise survival or future reproductive performance (Roff, 1993). At the population level, age at first reproduction drives population dynamics and contributes to population growth rate (Salguero-Gómez et al., 2016). Even small changes in this parameter may substantially affect population viability, particularly in long-lived species where generation times are extended (Jenouvrier et al., 2015).

Age at first reproduction is influenced by conditions experienced throughout an individual's pre-reproductive lifetime. Early-life conditions can have lasting consequences through developmental programming, where environmental conditions during critical developmental periods influence adult traits and performance (Douhard et al., 2013; Gluckman et al., 2005; Lindström, 1999). When favourable conditions enhance lifelong performance, these effects are often referred to as the 'silver spoon effect' (Grafen, 1988; Monaghan, 2008), manifesting as permanent changes in physiology, behaviour or morphology that influence both survival and reproductive timing (Birkhead, 2000; Reed et al., 2008). Conversely, adverse early conditions may result in developmental constraints that reduce reproductive potential throughout life (Metcalfe & Monaghan, 2001; Nettle et al., 2013).

Current environmental conditions at sexual maturity may also act as immediate proximate cues that influence breeding decisions through their effects on resource availability, body condition or social dynamics (McNamara et al., 2011; Monaghan, 2008; Williams, 1966). Unlike the lasting developmental effects of early-life conditions, these proximate cues operate as real-time signals that individuals use to assess whether conditions are favourable for initiating reproduction. Such current-condition effects are often mediated through body mass thresholds or breeding site availability (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009; Weimerskirch, 1992).

These early-life developmental effects and current environmental triggers can interact in complex ways (Monaghan, 2008). Individuals or cohorts may exhibit different sensitivities to current conditions depending on their early-life experiences (Douhard et al., 2014; Hammers et al., 2013). Such interactions can amplify responses when early-life and current conditions align (e.g. individuals from poor early environments being more sensitive to current stress), or generate compensatory mechanisms where favourable current environments overcome poor early conditions (Nettle et al., 2013). Understanding this dual influence is crucial for predicting population responses to environmental change, as these responses may depend not only on current conditions but also on the early-life experiences of recruiting cohorts (Jenouvrier et al., 2009; Sæther et al., 2013).

Multiple factors can influence age at first reproduction through these pathways, operating at birth, at sexual maturity, or anywhere in between (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009; Cam et al., 2003; Descamps et al., 2008; Lindström, 1999; Oro et al., 2008; Van De Pol et al., 2006; Weladji et al., 2008). Three main categories of drivers have been identified: demographic factors (e.g. population density and mate availability), environmental conditions and individual-level variation (Fay et al., 2016; Gamelon et al., 2016; Larue et al., 2015).

Population density can affect age at first reproduction through two distinct mechanisms with opposite outcomes. High density typically intensifies competition for resources, including food, delaying the attainment of critical body mass necessary to initiate reproduction (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009; Jorgenson et al., 1993; Krüger, 2005; Tavecchia et al., 2007; Votier et al., 2008; Weimerskirch, 1992). Competition for high-quality breeding sites and access to mates can further delay reproduction at very high densities (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009; Pardo et al., 2013). Conversely, at very low densities, Allee effects can delay reproduction when individuals have difficulty finding suitable breeding partners (Kokko & Rankin, 2006; Mourocq et al., 2016).

Environmental conditions may affect age at first reproduction both directly and indirectly through resource availability. Favourable conditions generally lead to earlier recruitment, as demonstrated in American goshawks (*Accipiter atricapillus*) where increased food availability accelerated recruitment (Krüger, 2005), and in red squirrels (*Sciurus vulgaris*) where spring spruce cone production is associated with early female recruitment (Descamps et al., 2006). In seabirds, large-scale climate oscillations affect recruitment timing through their influence on marine productivity and ocean conditions, with studies documenting delayed recruitment during unfavourable oceanographic periods (Frederiksen et al., 2006; Oro et al., 1999).

Individual heterogeneity, particularly sex, represents an intrinsic source of variation in age at first reproduction patterns. Sexual differences in life-history strategies often result in distinct recruitment ages, with males and females responding differently to the same demographic or environmental conditions (Fay et al., 2016; Stearns, 1992). For example, in sexually dimorphic seabirds, such as northern gannets (*Morus bassanus*), males typically recruit 1–2 years later than females (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009), while in red deer (*Cervus elaphus*), males delay reproduction relative to females due to higher costs of intrasexual competition (Metcalfe & Monaghan, 2001). In many long-lived species, sexual dimorphism in size, competitive ability or parental investment strategies can lead to sex-specific sensitivities to early-life conditions or current environmental factors (Metcalfe & Monaghan, 2001).

The wandering albatross (*Diomedea exulans*) population at Crozet (46° S; 52° E southern Indian Ocean) represents an excellent opportunity to investigate the drivers of age at first reproduction variation in a long-lived species. This population has been monitored for over five decades with extensive individual-based data. A sharp population decline (loss of 50% of the breeding population) was documented from 1970 until the mid-1980s, followed by a steady increase (Delord et al., 2008; Weimerskirch et al., 2018). Previous studies documented fluctuations in age at first reproduction across cohorts from 1970 to the mid-1980s (Weimerskirch et al., 2012), with a decrease from 12 to 10 years, between 1966 and 1982 (Weimerskirch, 1992). This decrease was hypothesized to result from reduced population density, which lowered competition for food resources. However, no formal quantitative study has investigated the demographic and environmental drivers of these changes in recruitment patterns.

In this study, we investigate the drivers of age at first reproduction variation in the wandering albatross population at Crozet. We test the following primary, and not mutually exclusive, hypotheses:

- Density-dependent effects at birth (H1): Age at first reproduction is affected by population density at birth through its influence on early-life conditions. Offspring development and reproduction can be delayed either through (a) a reduction in parental provisioning at higher densities due to competition or (b) reduced parental quality or provisioning at lower densities in a depleted population (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009; Votier et al., 2008). We acknowledge that if both high and low density produce delayed recruitment, distinguishing which mechanism dominates may be challenging. However, examining the directionality and strength of density effects across the observed population range can help identify the prevailing driver.
- Density-dependent effects at recruitment (H2): Age at first reproduction is influenced by mate availability in the years preceding first breeding. In wandering albatrosses, pair formation involves extended courtship and learning, during which young individuals prospect for partners and observe experienced breeders (Jouventin et al., 1999). Higher mate availability facilitates earlier breeding by reducing search costs and accelerating pair formation (Kokko & Rankin, 2006). In this population, male-biased sex ratio from female-biased fishery mortality may create asymmetric mate availability, with males experiencing greater competition and delayed recruitment when available females are limited.
- Environmental effects at birth (H3): Age at first reproduction is affected by environmental conditions during early life, consistent with silver spoon effects where favourable natal conditions enhance lifelong performance (Lindström, 1999; Monaghan, 2008). Wind patterns at birth may be particularly important, as wind drives parental foraging efficiency in wandering albatrosses (Weimerskirch, 2018), affecting chick provisioning and development. Favourable birth conditions should promote earlier recruitment through improved offspring condition (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009).
- Environmental effects at recruitment (H4): Age at first reproduction is influenced by environmental conditions during the recruitment period, as current conditions affect immediate breeding decisions in long-lived species (McNamara et al., 2011; Monaghan, 2008). The Indian Ocean subtropical anticyclone (Mascarene high) drives Southern Ocean wind patterns, and variations in its intensity and location can impact albatross foraging success, survival and breeding probability (Richardson & Wakefield, 2022; Xulu et al., 2020), thereby affecting recruitment timing.
- Sex-specific effects (H5): In wandering albatrosses, males typically recruit later than females (Weimerskirch, 1992), potentially reflecting higher thresholds for body condition or competitive ability required for successful pair formation. We expect sex-specific

responses to demographic and environmental conditions, as documented in other sexually dimorphic species (Metcalfe & Monaghan, 2001; Stearns, 1992).

2 | MATERIALS AND METHODS

2.1 | Study species and site

The wandering albatross population on Possession Island, Crozet Archipelago, has been studied since 1960, with annual mark–recapture efforts beginning in 1965 (Rouby, 2026b; Weimerskirch, 2018). The reproductive cycle spans almost 12 months, from pair formation in December to fledging in November (Tickell, 2000; Weimerskirch, 2018). Individuals begin breeding at a minimum age of 6 years once reaching sufficient body condition (Fay et al., 2016; Weimerskirch, 2018), and adults typically take a sabbatical year between breeding attempts to moult and regain body mass (Weimerskirch, 2018). Fledglings remain at sea in tropical and subtropical Indian Ocean waters for 3–7 years before returning to the colony (Weimerskirch, 1992; Weimerskirch et al., 2014).

Wandering albatrosses exhibit strong social monogamy with low divorce rates (females: 16% ± 1.6%; males: 9% ± 1%) (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). However, after mate loss, individuals often spend several years before re-pairing, reducing the population's overall reproductive rate (Jouventin et al., 1999; Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). Incidental fishery bycatch has been the primary driver of sex-biased mortality since the 1970s, disproportionately killing females and producing a male-skewed operational sex ratio with an accumulation of widowed males (Jouventin et al., 1999; Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022; Weimerskirch et al., 1987, 2005). The population declined from 500 breeding pairs in the 1960s to 240 pairs in the mid-1980s, recovered to 380 pairs in the 2000s, experienced a temporary decline after 2005 and has since stabilized at around 450 pairs (Delord et al., 2008; Weimerskirch et al., 2018).

2.2 | Data collection and monitoring protocol

The long-term monitoring of wandering albatrosses uses systematic capture–mark–recapture protocols where all individuals receive unique metal identification bands at birth. The colony is surveyed annually during the austral summer to identify breeders, record breeding status and success (egg laying, hatching and fledging), and document partner identities. Chicks are banded at 6 weeks of age, and morphometric measurements are taken annually on adults and fledglings, enabling complete individual life-history tracking from fledging through recruitment and subsequent breeding attempts. Monitoring effort was initially lower during programme establishment in the late 1960s–1970s, becoming more systematic in the early 1980s. Detection probability for breeders is very high (0.94, 95% CI: 0.92–0.95; Weimerskirch, 1992; see also Supporting Information S3—Figure S16), ensuring reliable identification throughout the study. This study included 11,166 individuals (5604 males and 5562 females) ringed as chicks between 1970 and 2005. The Crozet long-term demographic study has been continuously supported over six decades by Terres Australes et Antarctiques Françaises and the French Polar Institute IPEV (programme no.: 109), with field procedures approved by the IPEV Ethics Committee and the Comité de l'Environnement Polaire.

2.3 | Demographic and environmental covariates

We investigated how demographic factors and environmental conditions affect age at first reproduction through two temporal pathways: (1) conditions experienced at birth (cohort c), and (2) conditions experienced during the recruitment period (time t and lags $t-1$ to $t-3$). All analyses were conducted separately for males and females to assess sex-specific responses.

To investigate demographic effects, we used population density at birth and mate availability at recruitment. Population density was defined as the number of observed breeding pairs. We interpolated missing data for 1970–1974 and 1978–1980 using linear interpolation. This approach was appropriate given the gradual demographic changes expected in long-lived species and the documented monotonic population decline during this period (Delord et al., 2008; see Supporting Information S1—Figure S3). Excluding these years would have created gaps in cohort-specific analyses and reduced statistical power for detecting density effects at birth.

Mate availability was quantified as the ratio of individuals available for pairing to the number of established breeding pairs at the colony, capturing the relative intensity of mate-searching and competition for partners. The numerator included all pre-breeders aged 6+ years (physiologically mature but not yet recruited) plus widowed and divorced individuals observed at the colony (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022), regardless of sex. We tested mate availability at multiple time lags (t to $t-3$) because pair formation involves an extended prospecting and courtship period spanning multiple years before first breeding (Jouventin et al., 1999). Although this metric pools both sexes, mate availability may differ between males and females given the male-biased population structure, with males potentially experiencing stronger competition for partners. We therefore fitted separate models for each sex, allowing sex-specific responses to mate availability.

We selected five environmental variables based on their known influence on Southern Ocean conditions and seabird foraging ecology: the Indian Ocean Dipole (IOD), the El Niño Southern Oscillation (ENSO), and three metrics characterizing the Mascarene high pressure system (latitude, longitude and magnitude). The Indian Ocean Dipole affects sea surface temperatures and winds across the Indian Ocean, with positive IOD events predicted to improve foraging conditions through enhanced upwelling and productivity in wandering albatross foraging areas (Hameed, 2018). The El Niño Southern Oscillation affects global weather patterns and Southern Ocean productivity through its impact on upwelling patterns (Racault et al., 2017), with positive ENSO values generally predicted to reduce marine productivity and negatively affect seabird demographic rates (Ancona et al., 2011). The Mascarene high is a subtropical anticyclone whose geographical location and intensity strongly influence wind patterns across the Southern Ocean (Xulu et al., 2020). Given that wind conditions are critical for albatross flight efficiency and foraging success (Richardson & Wakefield, 2022; Weimerskirch, 2018), we predicted that northward latitude shifts would position stronger wind fields closer to foraging areas, eastern or western longitude shifts would affect access to productive upwelling zones, and stronger magnitude would generate more favourable wind conditions for efficient soaring flight. Environmental data were obtained from NOAA Physical Sciences Laboratory (https://psl.noaa.gov/data/climateindices/list/) for IOD and ENSO, and from NCEP/NCAR Reanalysis (https://psl.noaa.gov/data/gridded/data.ncep.reanalysis.html) for Mascarene high metrics.

2.4 | Analytical framework

Age at first reproduction is determined by two demographic processes: survival to reproductive age and the probability of breeding once mature. These vital rates shape recruitment patterns through distinct mechanisms. Survival determines whether individuals reach reproductive age, widening the distribution of potential recruitment ages. Breeding probability determines when surviving individuals actually recruit, compressing recruitment towards younger or older ages depending on whether early breeding is facilitated or suppressed. Demographic factors and environmental conditions can thus influence age at first reproduction through either pathway, and sex may modulate these relationships through different survival trajectories or breeding propensities.

We implemented a two-step analytical approach. First, we used hidden Markov models to estimate age- and cohort-specific survival and breeding probabilities while accounting for imperfect detection and state uncertainty. Second, we integrated these vital rates through absorbing Markov chains to calculate age at first reproduction and assess how demographic and environmental covariates influence it (Figure 1).

For all demographic and environmental covariates, we applied temporal windows appropriate to each vital rate. Covariates affecting survival were averaged over the full year (January–December), while those affecting breeding probability were averaged over the pre-breeding period (September–December), when conditions most influence body condition and breeding propensity. Early-life effects (cohort *c*) used covariate values from the birth year; current effects at recruitment (time *t*) used values from the prior year (*t* – 1). All variables were standardized (see Supporting Information S1—Figures S1–S4).

Although our capture–mark–recapture dataset extends to 2020, we restricted our analysis to cohorts born through 2005 because individuals can delay first reproduction up to 15 years (Weimerskirch, 1992). Including later cohorts would risk underestimating age at first reproduction by missing individuals that had not yet returned to recruit by 2020.

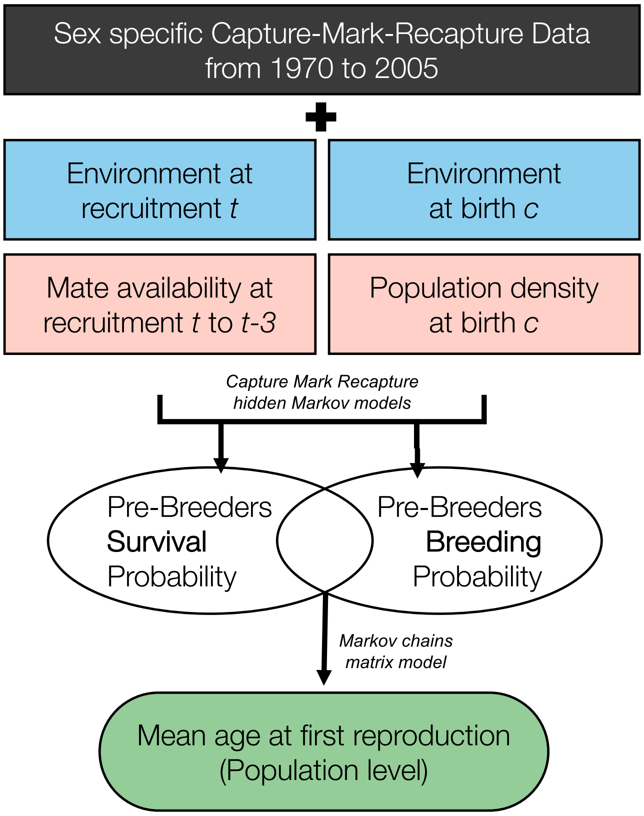

FIGURE 1 Analytical framework linking capture–mark–recapture data to age at first reproduction. Sex-specific capture–mark–recapture data from 1970 to 2005 (top) are analysed alongside demographic covariates (orange: population density at birth, mate availability at recruitment) and environmental covariates (blue: conditions at birth and recruitment). Hidden Markov Models account for imperfect detection to estimate age-specific pre-breeder survival and breeding probabilities (middle). These vital rates are integrated through absorbing Markov chain matrix models to calculate mean age at first reproduction at the population level (bottom).

2.5 | Multi-event capture–recapture models

2.5.1 | Life cycle and biological states

We used a hidden Markov model (Pradel, 2005) with seven biological states (six represented in Figure 2, the seventh being a 'dead' state) and five observable events. Transition and observation matrices, along with age-class specifications, are available in Supporting Information S2—Methods.

The seven biological states represent distinct stages in the albatross life cycle. Pre-Breeders (PB) are individuals up to age 15 that have not yet bred, including both physiologically immature and mature individuals that have not attempted reproduction. First

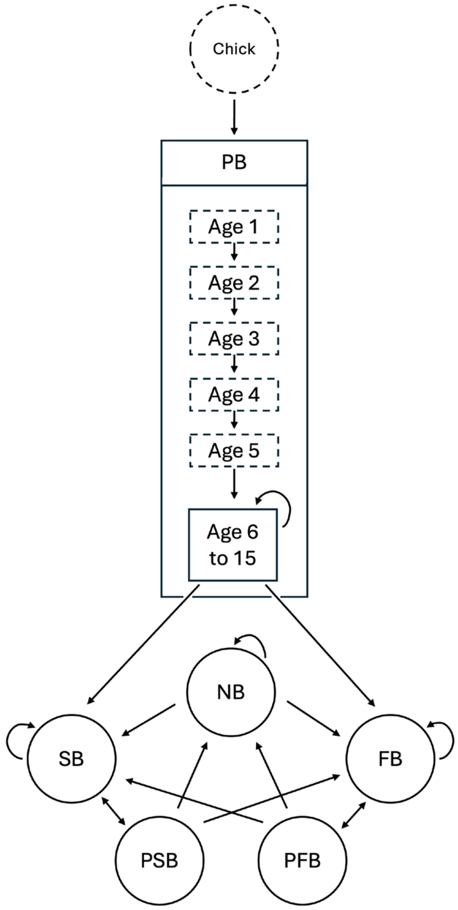

FIGURE 2 Wandering albatross life cycle. Chicks fledge at age 1 and enter the Pre-Breeder (PB) state until at least age 6. They then transition to Successful Breeder (SB), Failed Breeder (FB) or remain PB. By age 15, all individuals become either SB or FB. Post-breeding sabbaticals are categorized as Post-Successful Breeder (PSB) or Post-Failed Breeder (PFB). If an individual skips breeding again, it will reach the Non-Breeder (NB) state.

reproductions after age 15 are very unlikely and were not considered (Weimerskirch et al., 1987). Successful Breeders (SB) are adults (age 6+) that have bred at least once and successfully fledged a chick (Fay et al., 2016; Weimerskirch, 2018). Failed Breeders (FB) are adults (age 6+) that attempted breeding but did not fledge a chick, with mortality occurring at either the egg or chick stage. Post-Successful Breeders (PSB, age 7+) and Post-Failed Breeders (PFB, age 7+) are adults in their sabbatical year following a successful or failed breeding attempt, respectively. Non-Breeders (NB, age 8+) are adults that skip breeding even after the sabbatical year. Dead (D, age 2+) represents mortality.

The five observable events are: not detected (eND), detected as a successful breeder (eSB), detected as a failed breeder (eFB), detected as a breeder with unknown reproductive success (eB) and detected as non-reproductive (eNR), which includes both non-breeders and immature individuals.

Our models estimate demographic parameters (survival Φ and breeding probability Ψ) for each cohort (year of birth *c*) and age class (*a*), meaning all individuals born in the same year share the same age-specific vital rates. This cohort-based approach differs from traditional individual-based hidden Markov models, and formal goodness-of-fit tests are not applicable to this structure. However, previous analyses of this population using individual-based approaches support our modelling assumptions: Fay et al. (2015), Fay et al. (2016), Fay et al. (2017) found no evidence of trap-dependence in breeding adults, and transience during the pre-breeding stage is explicitly incorporated through our age-specific survival parameters.

2.5.2 | Temporal trends in demographic parameters

We conducted model selection based on WAIC (Vehtari et al., 2017) to identify the best model among 10 candidates designed to estimate temporal variation in survival and breeding probabilities across cohorts. Each model tested different hypotheses regarding trends in survival and/or breeding probabilities using the following general forms:

$$\mathrm{logit}(\Phi_{a,c}) = \mu_{a,1} + \beta_1 c + \beta_2 c^2 \tag{1}$$

for survival and

$$\mathrm{logit}(\Psi_{a,c}) = \mu_{a,2} + \gamma_1 c + \gamma_2 c^2 \tag{2}$$

for breeding probability, where *c* represents cohort year. For models testing only linear effects, the quadratic coefficients (β_2 and γ_2) were set to zero. For models with no temporal trends, both linear and quadratic coefficients were set to zero (see Supporting Information S2—Methods).

We did not include an interaction between age and cohort because this interaction is mathematically equivalent to time, which would confound cohort-specific effects with temporal variation. Although environmental conditions experienced by different cohorts could differentially affect age-specific demographic rates, this interaction cannot be separately identified from temporal effects. Our approach therefore assumes that cohort effects operate uniformly across age classes, which may not fully capture how early-life conditions influence age-specific vital rates throughout the pre-breeding period but avoids the identifiability issues inherent in age-cohort-time interactions.

Models ranged from $\mathcal{M}_0$, a baseline model accounting for random cohort variability without directional trends, to $\mathcal{M}_8$, which included quadratic trends in both survival and breeding probabilities. Our modelling framework contrasted two alternative explanations for temporal variation in age at first reproduction: Model $\mathcal{M}_0$ represented the null hypothesis that cohort-to-cohort differences arise from unstructured environmental stochasticity (random effects), while models $\mathcal{M}_1$ through $\mathcal{M}_8$ tested whether variation reflected systematic directional change (fixed trends). We did not combine random effects with fixed trends to avoid overfitting and to maintain a clear distinction between testing for directional trends versus characterizing random variation. If systematic trends exist, fixed trend models should outperform the random effects baseline; conversely, if variation is primarily stochastic, model $\mathcal{M}_0$ should be favoured. Model specifications are detailed in Supporting Information S2—Methods.

2.5.3 | Effects of demographic and environmental covariates on survival and breeding probabilities

We quantified the effects of demographic and environmental covariates on survival and breeding probabilities using the following equations, where *x* represents either birth year (*c*), recruitment year (*t*) or previous years (*t* – 1, *t* – 2, *t* – 3) for mate availability:

$$\text{logit}(\Phi_{a,x}) = \mu_{a,1} + \beta \text{COV}_x + \upsilon_x \qquad (3)$$

$$\text{logit}(\Psi_{a,x}) = \mu_{a,2} + \gamma \text{COV}_x + \upsilon_x \qquad (4)$$

where μ represents the age-specific intercept, β and γ represent the linear effect sizes for survival and breeding probability, respectively, COV_x is the standardized covariate value at time *x* and υ represents random effects.

Although theory suggests potential non-linear density-dependent effects (e.g. H1), we used linear covariate effects to maintain model parsimony and computational feasibility. Quadratic effects were explored only for temporal trends across cohorts.

2.6 | Age at first reproduction estimation

2.6.1 | Absorbing Markov chains

We estimated age at first reproduction and its temporal variation using absorbing Markov chains (Caswell, 2001; Roth & Caswell, 2018). Using demographic rates estimated from the hidden Markov models, we constructed transition matrices for each cohort and for credible covariates (covariates for which the 95% posterior distribution of β or γ excluded zero; Jenouvrier et al., 2018). Failed Breeders and Successful Breeders were set as absorbing states, meaning the iterative process ceased once individuals reached either state. Age at first reproduction was calculated as the expected time to reach these absorbing states from the initial pre-breeder state at fledging. To propagate uncertainty, we performed Markov chain calculations across the full posterior distributions of demographic rates from the hidden Markov models, generating 95% credible intervals for all age at first reproduction estimates. Absorbing Markov chain analyses were performed using MATLAB (The MathWorks Inc., 2021).

2.6.2 | Model implementation and diagnostics

Demographic parameter estimation was carried out using Markov Chain Monte Carlo (MCMC) with `nimble` version 1.01 (de Valpine et al., 2017; Turek et al., 2016) in `R` version 4.3.1 R Core Team (2021). Prior specifications and model details are, respectively, available in Table S1 and Supporting Information S2—Methods. All models achieved satisfactory convergence with proper chain mixing (Gelman & Rubin, 1992; Gelman et al., 2013), as verified through MCMC trace plots, $\hat{R}$ statistics ($\hat{R} < 1.05$;) and posterior density plots (Supporting Information S3—Figures S6–S11). Code is available at https://github.com/etienneroubyINSTAAR/AFR-WA-JAE2025.

3 | RESULTS

3.1 | Temporal changes in age at first reproduction

The best-fitting models were $\mathcal{M}_2$ (survival: no trend / breeding: quadratic trend) for males and $\mathcal{M}_8$ (survival: quadratic trend / breeding: quadratic trend) for females (Supporting Information S3—Table S2 for WAIC selection). Complete demographic parameter estimates (survival, breeding and detection probabilities) from the best-fitting models are presented in Supporting Information S3—Figures S12–S16.

Capture–recapture analysis revealed clear temporal patterns in age at first reproduction (Figure 3) with a decline from 9.2 to 7.8 years in females, and from 10.5 to 9.2 in males, followed by an increase to 8.2 and 9.8 years, respectively, by 2005. Males consistently began breeding about 1 year later than females throughout the study period.

Observed mean age at first reproduction values showed greater variability in early cohorts (1970–1975) where sample sizes were smallest ($n < 100$ individuals per cohort-sex), while closer agreement between observed and model-estimated values occurred in cohorts with larger sample sizes ($n < 200$).

3.2 | Effects on survival and breeding probabilities

3.2.1 | Demographic effects

There were consistent positive effects of mate availability on breeding probability for pre-breeders of ages 6 to 15, for both sexes across multiple time lags (Figure 4). For females, the effect sizes of mate availability were 0.34 (95% CI: 0.12–0.57) at *t* – 1, 0.31 (95% CI: 0.11–0.48) at *t* – 2 and 0.38 (95% CI: 0.20–0.57) at *t* – 3. Males showed similar positive effects, with effect sizes of 0.22 (95% CI: 0.01–0.41) at *t* – 1, 0.21 (95% CI: 0.03–0.41) at *t* – 2 and 0.22 (95% CI: 0.02–0.41) at *t* – 3.

In contrast, population density (number of breeding pairs) at birth had a negative effect on breeding probability for males (−0.15,

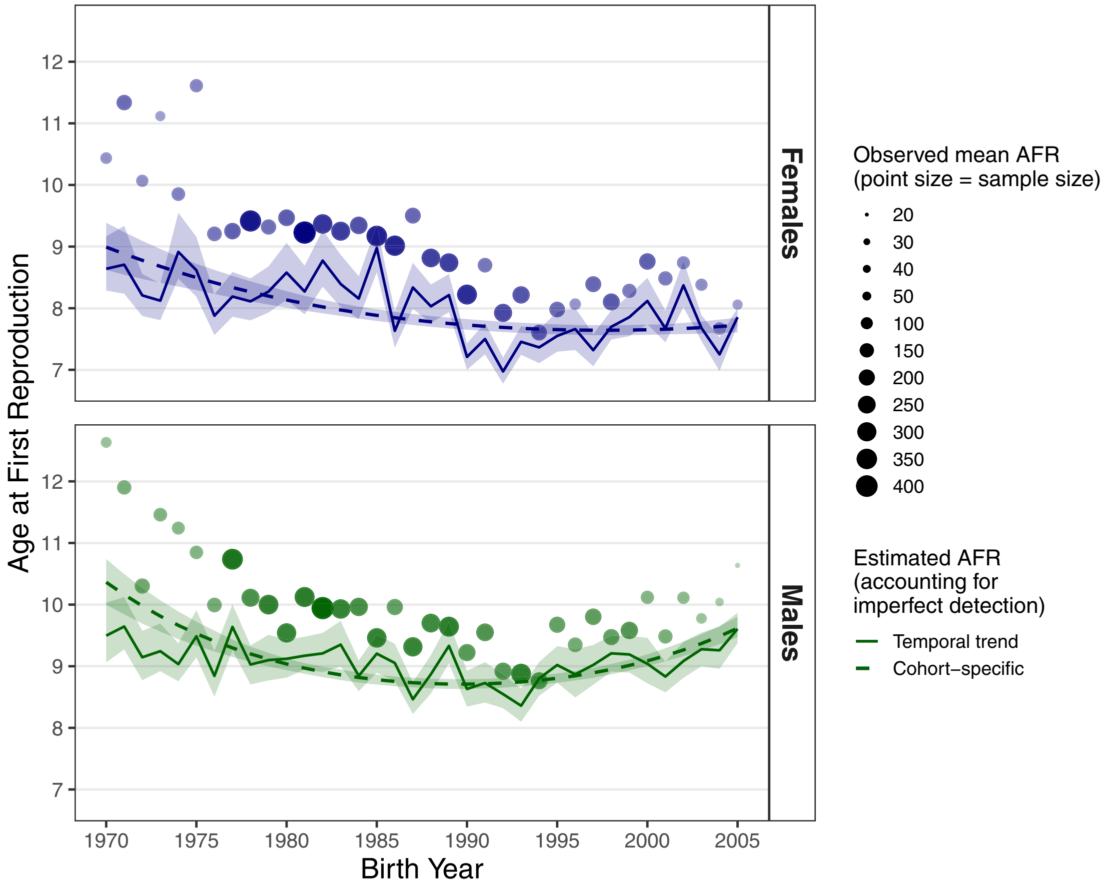

FIGURE 3 Temporal patterns in age at first reproduction. Age at first reproduction (AFR in legends) for male and female cohorts from 1970 to 2005. Points represent observed mean age at first reproduction from raw data, with point size and transparency proportional to sample size (*n* ranging from 22 to 426 individuals per cohort-sex combination). Smaller, more transparent points indicate cohorts with limited data, particularly in early years. Lines show model estimates from capture–recapture analysis that account for imperfect detection: Dashed lines represent temporal trends while solid lines show cohort-specific effects, with 95% credible intervals (shaded areas). Both observed points and model estimates share the same *Y*-axis scale (in years). Discrepancies between observed points and model estimates, especially in early cohorts with small sample sizes, reflect imperfect detection and sampling limitations that are corrected by the capture–recapture framework.

95% CI: −0.28 to −0.05) but not for females (−0.07, 95% CI: −0.23 to 0.09).

3.2.2 | Environmental effects

Analysis of environmental effects on survival and breeding probabilities of pre-breeders revealed that only conditions experienced at birth yielded 95% credible intervals (CI) not overlapping zero (Figure 5).

ENSO conditions at birth showed the strongest influence, with credible positive effects on breeding probabilities of females (effect size = 0.24, 95% CI: 0.09 to 0.39) and males (effect size = 0.15, 95% CI: 0.03 to 0.27). Mascarene high magnitude at birth also had a positive credible effect on breeding probabilities for females (effect size = 0.25, 95% CI: 0.06 to 0.38) and for males (effect size = 0.12, 95% CI: 0.02 to 0.23). Mascarene high latitude at birth had a positive credible effect only on male survival (effect size = 0.12, 95% CI: 0.07 to 0.17). In contrast, no environmental variables experienced at recruitment showed credible effects on either breeding probability or survival for either sex, as all 95% CIs included zero.

3.3 | Demographic and environmental effects on age at first reproduction

Population density at birth and mate availability at recruitment showed distinct effects on recruitment between sexes (Figure 6). Mate availability had a negative effect on age at first reproduction for both females and males, indicating that higher mate availability corresponded to earlier reproduction. The effect appeared stronger for females, with age at first reproduction decreasing from about 10.75 to 8.25 years across the range of standardized mate availability values, compared with a decrease from approximately 11.5 to 9.75 years for males. Population density at birth showed contrasting effects between sexes. For males, but not for females, there was a

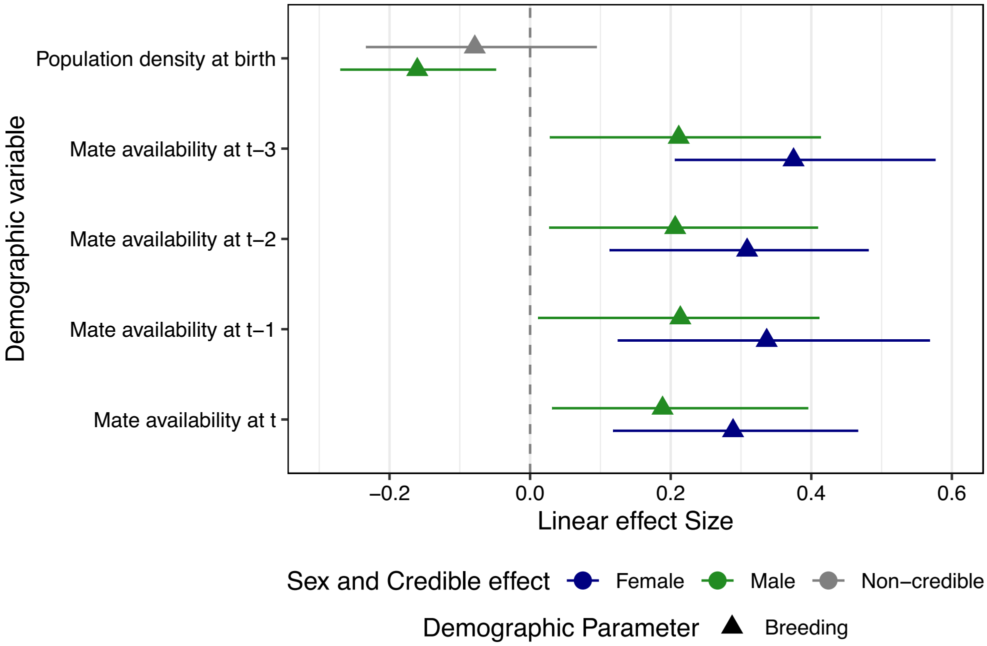

FIGURE 4 Effects of population density and mate availability on breeding probability of pre-breeders. Linear effect sizes of mate availability are evaluated at different time lags (*t* to *t* − 3) and population density at birth. Blue and green triangles represent credible effects for females and males, respectively, while grey indicates non-credible effects. Error bars show 95% credible intervals.

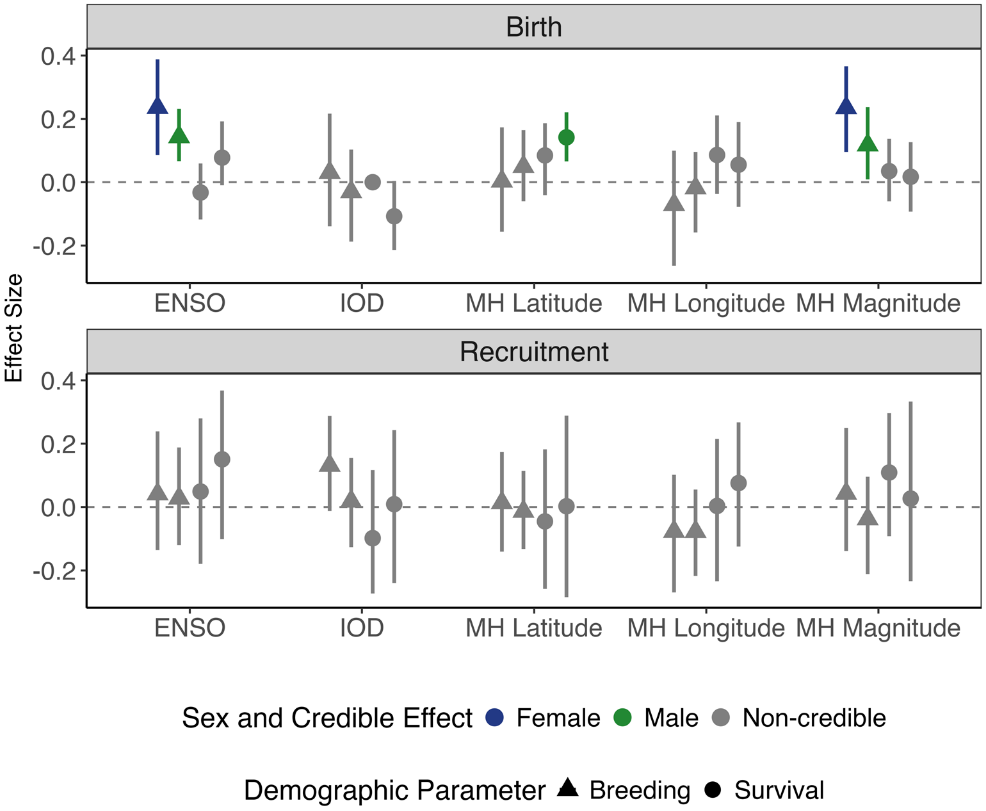

FIGURE 5 Effects of environmental variables on survival and breeding probabilities of pre-breeder wandering albatrosses. Effects of five environmental variables—Indian Ocean Dipole (IOD), El Niño Southern Oscillation (ENSO) and three Mascarene high metrics (latitude, longitude and magnitude)—tested at birth (top) and recruitment (bottom) show the temporal window during which these covariates influence vital rates. Points show mean effects with 95% credible intervals. Credible effects (intervals excluding zero) are in blue for females and green for males. Triangles indicate breeding probability, circles indicate survival.

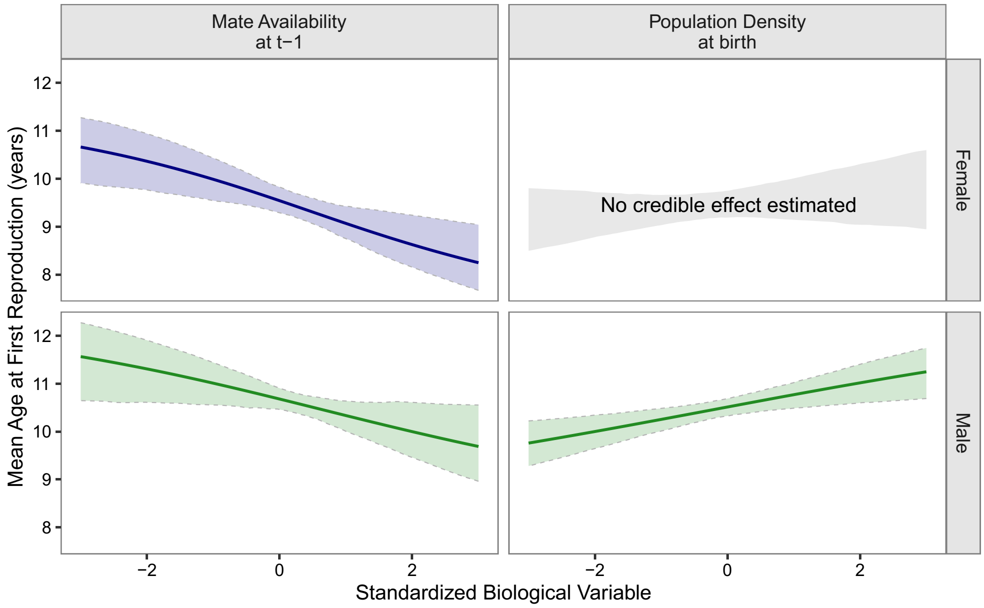

FIGURE 6 Effects of demographic variables on age at first reproduction. The figure shows the effect of standardized mate availability at t-1 and population density at birth on mean age at first reproduction for females (top row, blue) and males (bottom row, green). Solid lines represent mean effects, with shaded areas indicating 95% confidence intervals. Only mate availability at *t*-1 is shown, as results were similar for each time lag. Population density at birth effect on female age at first reproduction was not credible. It is displayed in grey to contrast with credible effects.

positive relationship between population density at birth and age at first reproduction, with a decrease from about 9.75 to 11.5 years across the range of standardized density values.

The effects of environmental variables at birth on age at first reproduction varied across factors and between sexes (Figure 7 and see Supporting Information S3—Figures S5 for raw correlations). ENSO conditions at birth showed a strong negative relationship with age at first reproduction for both females and males, with higher ENSO values being associated with earlier reproduction. The effect appeared slightly stronger for females, with age at first reproduction decreasing from approximately 10.5 to 8.5 years across the range of standardized ENSO values, compared with a decrease from about 11.0 to 9.5 years for males. Mascarene high magnitude at birth also exhibited a negative relationship with age at first reproduction for both sexes, with a similar magnitude to ENSO. In contrast, Mascarene high latitude at birth showed little to no effect on age at first reproduction for either sex.

4 | DISCUSSION

Using a 35-year individual-based dataset, we investigated how environmental conditions and demographic factors shape recruitment in wandering albatrosses. Three main findings emerged. First, age at first reproduction declined markedly from the 1970s to the mid-1980s before stabilizing, with consistent sex-specific differences throughout. Second, environmental conditions experienced at birth, but not at recruitment, influenced age at first reproduction through effects on breeding probability rather than survival. Third, mate availability during the prospecting period strongly facilitated earlier recruitment in both sexes, while natal density delayed recruitment in males only. This asymmetry between early-life and current environmental effects is striking. It suggests that recruitment timing in this long-lived seabird is shaped primarily by developmental programming during the natal period rather than by immediate environmental triggers at sexual maturity, consistent with silver spoon effects (Monaghan, 2008). However, the strong influence of mate availability demonstrates that social context during the prospecting phase modulates these early-life effects (Jouventin et al., 1999).

4.1 | Demographic factors

4.1.1 | Population density

Natal population density affected male, but not female, recruitment timing. This sex-specific response exemplifies a fundamental principle in life-history evolution: when sexes differ in reproductive costs or competitive pressures, natural selection favours divergent sensitivities to conditions during development (Bonduriansky & Chenoweth, 2009; Stearns, 1992). Such developmental plasticity has been documented across taxa. In mammals, males are often more sensitive to maternal nutritional stress than females, likely because their faster growth rates and larger adult size make them more vulnerable to resource limitation during critical developmental windows (Metcalfe & Monaghan, 2001). The timing of sex-specific developmental spurts can determine which sex bears greater costs under poor conditions (Metcalfe &

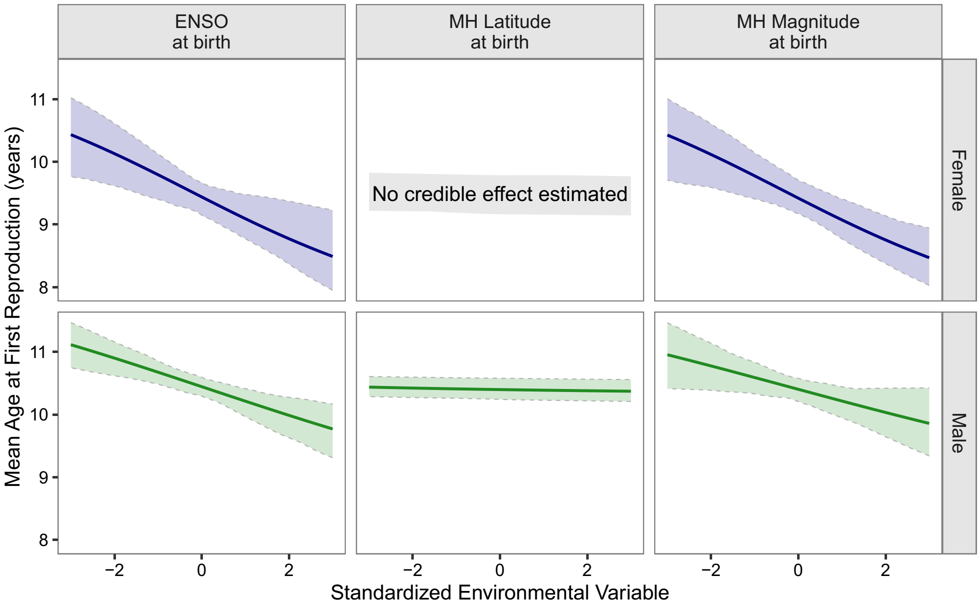

FIGURE 7 Effects of environmental variables at birth on age at first reproduction. Effects of standardized ENSO, Mascarene high latitude, and magnitude at birth on mean age at first reproduction for females (top, blue) and males (bottom, green). Solid lines show mean effects, with shaded areas indicating 95% confidence intervals. Mascarene high latitude at birth effect on female age at first reproduction was not credible. It is displayed in grey to contrast with credible effects.

Monaghan, 2001). In colonial seabirds, breeding density affects parental provisioning strategies and chick survival (Ashbrook et al., 2010), with density-dependent competition influencing resource availability and population growth (Pulvirenti et al., 2023).

In wandering albatrosses specifically, males are larger and mature later than females, requiring greater body mass to initiate breeding (Weimerskirch, 1992, 2018). High natal population density may constrain offspring development through intensified intraspecific competition for resources in central-place foraging systems (Ashbrook et al., 2010; Pulvirenti et al., 2023), where breeding adults concentrate foraging effort in accessible areas. Males, with their higher energetic requirements during the extended rearing period (Weimerskirch et al., 2005), may be more vulnerable to resource limitation when competition is intense. Females, with their lower weight threshold for breeding onset and earlier maturation (Weimerskirch, 1992), appear buffered against such density effects during development. This sex-specific vulnerability to natal conditions has important demographic consequences: male recruitment will be more sensitive than female recruitment to fluctuations in population density during the rearing period, potentially generating sex-biased cohort effects in response to environmental change.

4.1.2 | Mate availability

In species with extended pair bonding periods, the pool of available partners may constrain when individuals can successfully recruit. This is particularly relevant in systems where low population density or skewed sex ratios create Allee effects through difficulties in finding mates (Kokko & Rankin, 2006). For wandering albatrosses, pair formation is protracted, taking an average of 3.2 years for males and 2.3 years for females (Jouventin et al., 1999), during which inexperienced birds display at colonies and assess potential partners (Jouventin et al., 1999).

Mate availability strongly influenced recruitment timing in our study population, with effects apparent across multiple time lags (*t* to *t* − 3). Higher availability was consistently associated with earlier breeding. These multi-year lagged effects likely reflect the extended pair formation process described above (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). An alternative explanation is temporal autocorrelation: years of high mate availability tend to be followed by years of similarly high availability, creating apparent lagged effects. Regardless of mechanism, these strong mate availability effects occurred during a period of population recovery from severe depletion (Delord et al., 2008; Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022), when the number of pre-breeding individuals increased faster than the number of established breeding pairs (Supporting Information S1—Figures S3). This demographic shift facilitated earlier recruitment, demonstrating how population structure (not just individual condition or environmental quality) shapes life-history transitions. Such demographic coupling means that perturbations affecting adult demographic rates will have delayed but substantial effects on recruitment patterns.

4.2 | Environmental conditions

Environmental conditions at recruitment showed no effect on age at first reproduction, in stark contrast to natal conditions. Theory predicts that current environmental conditions should act as proximate cues influencing breeding decisions through their effects on resource availability and body condition (Monaghan, 2008). Yet, environmental conditions experienced at birth (but not at recruitment) determined when individuals bred for the first time. This asymmetry supports the developmental programming hypothesis, whereby early experiences create lasting phenotypic effects that override immediate environmental triggers (Gluckman et al., 2005; Metcalfe & Monaghan, 2001).

Two atmospheric-oceanic systems influenced recruitment timing through their effects during the natal year. ENSO conditions at birth affected breeding probability in both sexes, likely operating through marine productivity (Racault et al., 2017). While El Niño events alter Southern Ocean upwelling patterns, regional responses vary and enhanced productivity in some areas may improve prey availability for provisioning parents, with lasting effects on offspring condition and subsequent recruitment. Mascarene high magnitude at birth also positively affected breeding probability. This subtropical anticyclone system drives wind patterns across the Southern Ocean; stronger systems generate more favourable wind conditions for efficient soaring flight (Richardson et al., 2018), potentially enabling parents to access more distant foraging areas and provision offspring more effectively (Weimerskirch, 2018). For central-place foragers like wandering albatrosses (during breeding season), where parents are constrained to return to breeding colonies, environmental conditions that facilitate foraging efficiency can have substantial effects on offspring provisioning and development (Pulvirenti et al., 2023). Although we hypothesized that shifts in the Mascarene high's position (latitude and longitude) would also affect foraging ecology by altering access to productive upwelling zones and frontal systems (Weimerskirch, 2018), we found no credible effects of these positional metrics.

These results align most closely with the silver spoon hypothesis (Lindström, 1999; Monaghan, 2008): Favourable early-life conditions conferred lifelong advantages, with individuals experiencing beneficial natal environments recruiting earlier regardless of conditions at sexual maturity. Testing alternative frameworks would require different study designs. The predictive adaptive response (PAR) hypothesis (Bateson et al., 2014; Gluckman et al., 2005) predicts interactive effects between early-life and current conditions, where organisms develop phenotypes matched to their anticipated adult environment based on early-life cues. Fitness is maximized when the predicted environment matches the experienced environment, but mismatches between early cues and later reality incur fitness costs (Bateson et al., 2014). The environmental saturation hypothesis (Engqvist & Reinhold, 2016; Pigeon et al., 2019) proposes that early-life effects on fitness are strongest under intermediate adult conditions, but become suppressed under extreme environments—either because all individuals perform poorly in harsh conditions (detrimental saturation) or because all perform well in favourable conditions (beneficial saturation). Our study lacked the explicit early-life × recruitment environment interactions required to test PAR and the extreme environmental variation necessary to detect saturation effects. However, an important caveat is that we defined 'early-life' strictly as the natal year and 'current' as the recruitment period. Monaghan's (2008) framework emphasizes that individuals from different early environments may show varying sensitivities to current stressors through interactive effects: a more nuanced prediction than simple main effects, which our design could not test.

4.3 | Sex-specific differences

Males consistently recruited 1–2 years later than females across all cohorts (Figure 3), expanding on earlier findings from this population (Weimerskirch, 1992). Weimerskirch (1992) documented that females first returned to the colony at age 5.7 years versus 6.2 years for males, and first bred at 9.6 versus 10.4 years, respectively. This persistent sex difference occurs despite strong assortative mating by age in established pairs (Jouventin et al., 1999), indicating that factors beyond physiological maturity constrain when each sex can successfully initiate breeding.

Body condition thresholds provide a partial explanation. Non-breeding males average 9.3 kg while breeding males average 10.1 kg and females show similar patterns but at lower absolute weights (7.4 vs. 8.1 kg; Weimerskirch, 1992). Males thus face a higher weight threshold to initiate breeding, requiring more time to accumulate the necessary condition. This sex difference in threshold likely reflects the greater energetic costs of rearing male offspring, which require more food during their extended 8-month growth period (Weimerskirch et al., 2005). However, body condition alone cannot fully explain recruitment timing variation. Fay et al. (2016) demonstrated that earlier-recruiting individuals of both sexes subsequently showed higher survival and reproductive performance throughout life, suggesting that recruitment age reflects underlying individual quality rather than alternative life-history strategies.

The male-biased operational sex ratio, driven by female-biased fishery mortality (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022), creates asymmetric mating opportunities that further delay male recruitment. In such systems, females can be more selective. First-time breeding females preferentially select males with greater experience (Jouventin et al., 1999), and females exhibit higher divorce rates in this male-skewed population (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022), demonstrating continued mate selectivity. Males, facing stronger intrasexual competition for the limited pool of females, experience longer pair formation periods (3.2 years on average versus 2.3 years for females; Jouventin et al., 1999). The male-skewed operational sex ratio intensifies male–male competition, with intruder males actively disrupting established pairs (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). These demographic constraints amplify sex-specific competition, generating recruitment delays that reflect social constraints as much as developmental ones. The pattern does not contradict assortative mating (Jouventin et al., 1999), but illustrates how demographic context modulates when individuals can successfully transition from physiological readiness to actual breeding initiation.

4.4 | Methodological considerations

We decomposed age at first reproduction into its underlying vital rates (survival and breeding probability) using hidden Markov models, then integrated these through absorbing Markov chains (Caswell, 2001). This two-step approach provided insights that direct estimation of recruitment age would have missed. Most importantly, it revealed which demographic process mediates demographic and environmental effects on recruitment. For example, natal environmental conditions (ENSO, Mascarene high magnitude) influenced recruitment timing exclusively through breeding probability, not survival. While Mascarene high latitude at birth affected male survival (Figure 5), this did not translate to effects on age at first reproduction (Figure 7), indicating compensatory dynamics across vital rates. This framework also naturally accommodates imperfect detection and state uncertainty inherent in capture–recapture data, and propagates uncertainty by computing age at first reproduction across the full posterior distributions of vital rates.

We deliberately excluded age-dependence among established breeders from our models. Our focus was on drivers of recruitment timing, not post-recruitment trajectories. However, age at first reproduction likely influences subsequent demographic rates. In kittiwakes, early recruits showed faster reproductive senescence than late recruits (Aubry, Cam, & Monnat, 2009; Aubry, Koons, et al., 2009), and similar patterns linking recruitment decisions to breeding trajectories occur across seabirds. Future work could integrate recruitment timing with post-recruitment performance to assess whether the factors delaying recruitment in wandering albatrosses also shape later-life demographic rates.

4.5 | Broader implications for seabird ecology and life-history theory

Rapid environmental change is altering the conditions seabirds experience during development, yet predicting how recruitment will respond requires understanding which environmental windows matter and through what mechanisms. Our results reveal a striking temporal asymmetry: natal environmental conditions (experienced potentially a decade before recruitment) shaped when individuals bred, while conditions during sexual maturity had no detectable effect. This developmental programming occurred exclusively through breeding probability, with survival buffered against environmental variation. Such canalization of survival, the vital rate most strongly linked to fitness in long-lived species, exemplifies demographic buffering (Gaillard & Yoccoz, 2003). Plasticity in breeding decisions allows reproductive timing to respond to early-life experience without compromising survival, a pattern documented across long-lived taxa (Gaillard et al., 2000).

Demographic structure imposed additional constraints that interacted with these environmental effects. High natal density delayed male (but not female) recruitment, likely through reduced provisioning during development (Weimerskirch, 1992). Yet, during the prospecting phase, higher mate availability (itself a product of demographic perturbations) facilitated earlier recruitment in both sexes (Jouventin et al., 1999). Density thus simultaneously constrained recruitment (through early-life competition) and facilitated it (through partner availability), operating at different life stages through different mechanisms. The multi-year lags in mate availability effects (t to $t-3$) demonstrate that recruitment decisions integrate demographic information accumulated during the extended prospecting period, not just immediate conditions at sexual maturity.

These findings have implications for predicting population responses to environmental change. Because natal conditions (not recruitment-period conditions) determine when individuals breed, cohorts experiencing poor environmental conditions during development will show delayed recruitment years later, regardless of conditions when they reach maturity. In wandering albatrosses, where individuals recruit at 9–10 years on average and can delay first reproduction up to 15 years (Weimerskirch, 1992), such cohort effects persist for over a decade, creating lagged demographic responses to environmental perturbations. Sex-biased mortality from fisheries further complicates predictions by altering mate availability and generating sex-specific recruitment delays. Understanding recruitment therefore requires tracking environmental conditions, demographic structure and their interactions across the entire prebreeding period. A challenge for species experiencing rapid environmental change in increasingly human-impacted oceans.

AUTHOR CONTRIBUTIONS

Etienne Rouby, Joanie Van de Walle and Stéphanie Jenouvrier conceived the project. Joanie Van de Walle and Stéphanie Jenouvrier obtained the funding. Karine Delord, Henri Weimerskirch and Christophe Barbraud provided data. Etienne Rouby and Floriane Plard performed analyses. Henri Weimerskirch, Christophe Barbraud, Lise M. Aubry, Timothée Bonnet, Karine Delord, Joanie Van de Walle and Stéphanie Jenouvrier provided expertise in wandering albatross ecology and life-history interpretation. All authors contributed to the interpretation of results. Etienne Rouby led the writing, and all authors contributed to revising the text.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the InDoRES Digital Repository https://doi.org/10.48579/PRO/HCNYDV (Rouby, 2026a).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Temporal variation in environmental covariates used for survival analysis (1970–2020). Time series show ENSO (El Niño Southern Oscillation), IOD (Indian Ocean Dipole), MH Lat (Mascarene high Latitude), MH Lon (Mascarene high Longitude) and MH M (Mascarene high Magnitude). Environmental variables were averaged over the full year (January to December) for survival analyses and standardized before analysis.

Figure S2. Temporal variation in environmental covariates used for breeding analysis (1970–2020). Time series show the same variables as Figure 1 but averaged over the pre-breeding season (September to December) as these conditions are most likely to affect breeding decisions. All variables were standardized before analysis.

Figure S3. Population size dynamics of wandering albatross breeding pairs at Crozet (1960–2020). The population declined from approximately 500 pairs in the 1960s to 240 pairs in the mid-1980s, recovered to 380 pairs in the 2000s, experienced a temporary decline after 2005 and subsequently recovered to current levels of around 450 pairs. Missing data for 1970–1974 and 1978–1980 were interpolated using linear interpolation.

Figure S4. Mate availability index over time (1970–2012). Mate availability was calculated as the ratio of potential mates (pre-breeders ≥ 6 years old plus widowed and divorced individuals from both sexes) to the total breeding population. The index shows an overall increasing trend, indicating improved mate availability during population recovery, with some fluctuations reflecting demographic stochasticity.

Table S1. Prior distributions and MCMC specifications.

Table S2. Model selection for temporal trends in pre-breeder survival and breeding probabilities using WAIC. Models are ranked from best (lowest WAIC) to worst within each sex. The × symbol indicates which components are included in each model. Random effects (Rand.) represent unstructured cohort-to-cohort variation, while linear (Lin.) and quadratic (Quad.) trends represent directional temporal changes. pWAIC represents the effective number of parameters measuring the effective complexity of each model.

Figure S5. Relationships between age at first reproduction and environmental and biological covariates by sex. Each panel shows the relationship between mean age at first reproduction and standardized covariate values for females (top row) and males (bottom row). Points represent cohort-specific mean age at first reproduction values, with point size proportional to sample size (number of individuals per cohort). Lines show linear regression fits with 95% confidence intervals (grey shading). Environmental covariates include the El Niño Southern Oscillation (ENSO) Index and Mascarene high atmospheric pressure system parameters (latitude, longitude and magnitude). The biological covariate represents population size (number of breeding pairs) at the time of birth. We did not represent the Indian Ocean Dipole (IOD) index because it had no effect at birth. We also did not represent mate availability because we do not test it at birth in the study. All covariates were standardized (z-score) prior to analysis. Cohorts span from 1970 to 2005.

Figure S6. MCMC trace plots for some parameters of female best-fitting model ($\mathcal{M}_8$). Trace plots show good mixing and convergence for all parameters across three MCMC chains (different colours). All parameters achieved $\hat{R} < 1.05$, indicating satisfactory convergence. b1phiPB is linear effect of cohort on survival; b2phiPB is quadratic effect of cohort on survival; pB1 is detection probability of Successful breeders; pPB1 is detection probability of first age-class Pre-Breeders; b1psiPB is linear effect of cohort on breeding probability; b2psiPB is quadratic effect of cohort on breeding probability; phiPB1 is the intercept for survival of first age-class Pre-breeders; psiPB1 is the intercept for breeding probability of first age-class Pre-Breeders.

Figure S7. MCMC trace plots for some of parameters of male best-fitting model ($\mathcal{M}_2$). Similar to Figure S6, showing excellent chain mixing and convergence for the male-specific model. The male model included quadratic trends in breeding probability but no quadratic temporal trends in survival probability. b1phiPB is linear effect of cohort on survival; b2phiPB is quadratic effect of cohort on survival; pB1 is detection probability of Successful breeders; pPB1 is detection probability of first age-class Pre-Breeders; b1psiPB is linear effect of cohort on breeding probability; b2psiPB is quadratic effect of cohort on breeding probability; phiPB1 is the intercept for survival of first age-class Pre-breeders; psiPB1 is the intercept for breeding probability of first age-class Pre-Breeders.

Figure S8. Posterior density plots for some selected female model parameters. Overlapping posterior densities from three independent MCMC chains demonstrate good convergence and proper mixing.

The smooth, unimodal distributions indicate well-identified parameters with sufficient data support. Not all parameters are displayed. See Figure S10 to assess all parameters convergence.

Figure S9. Posterior density plots for some selected male model parameters. Posterior distributions show similar convergence properties to the female model, with overlapping densities across chains confirming reliable parameter estimation. Not all parameters are displayed. See Figure S11 to assess all parameters convergence.

Figure S10. $\hat{R}$ convergence diagnostics for all monitored parameters in female model. All parameters show $\hat{R}$ values below 1.05 (indicated by dashed red line), confirming convergence. Values close to 1.0 indicate excellent convergence, while the threshold of 1.05 represents acceptable convergence for reliable inference.

Figure S11. $\hat{R}$ convergence diagnostics for all monitored parameters in male model. Similar to the female model, all parameters meet the convergence criterion of $\hat{R} < 1.05$, ensuring reliable parameter estimates for subsequent inference about age at first reproduction patterns.

Figure S12. Pre-breeder survival probability by age and birth cohort. Survival estimates from best-fitting models show age-dependent patterns with lower survival in the first 2 years of life, followed by high survival during the pre-breeding period. Different lines represent different birth cohorts (1970–2005), showing temporal variation in survival across cohorts for both females (left) and males (right). Shaded areas represent 95% credible intervals.

Figure S13. Pre-breeder breeding probability by age and birth cohort. Breeding probability estimates show the characteristic age-dependent pattern of recruitment, with very low probabilities at young ages (6–8 years) followed by rapid increases. The peak around age 8–10 reflects the modal age at first reproduction. Temporal trends show cohort-specific variation in breeding probability, particularly for males (right panel) where later cohorts show delayed breeding patterns.

Figure S14. Pre-breeder reproductive success probability by age and birth cohort. Breeding success (probability of fledging a chick given a breeding attempt) for first-time breeders increases from 6 to 10 years in both sex. No cohort effects where tested for breeding success.

Figure S15. Pre-breeder detection probability by age and birth cohort. Detection probability estimates show the expected age-dependent pattern, with very low detection at young ages when birds are at sea, followed by increasing detection as birds begin prospecting at the colony. The peak detection occurs around ages 7–9 when pre-breeders regularly visit the colony before first breeding. No cohort effects were tested on detection probability.

Figure S16. Adult demographic parameters by breeding state. Point estimates with 95% credible intervals for survival probability (left), breeding probability (middle left), reproductive success probability (middle right) and detection probability (right) for different adult breeding states. SB = Successful Breeder, FB = Failed Breeder, PSB = Post-Successful Breeder, PFB = Post-Failed Breeder, NB = Non-Breeder. Results show expected patterns with high survival across all states, variable breeding probabilities depending on previous breeding experience and high detection for breeding individuals.

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