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Review Article

Stranding-Based Demographic Inference in Marine Mammals: Best Practices for Extracting Vital Rates Despite Compound Sampling Bias

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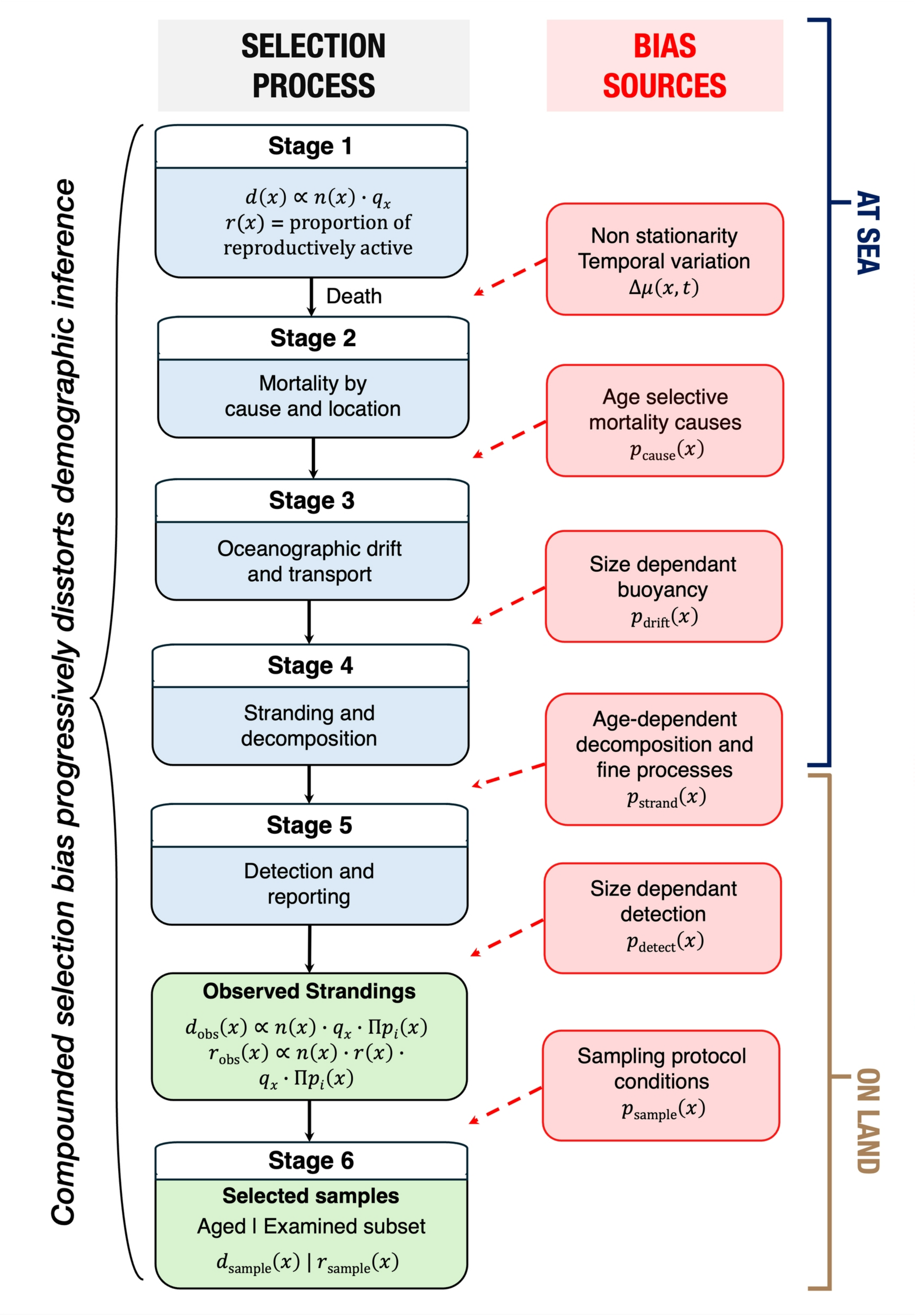
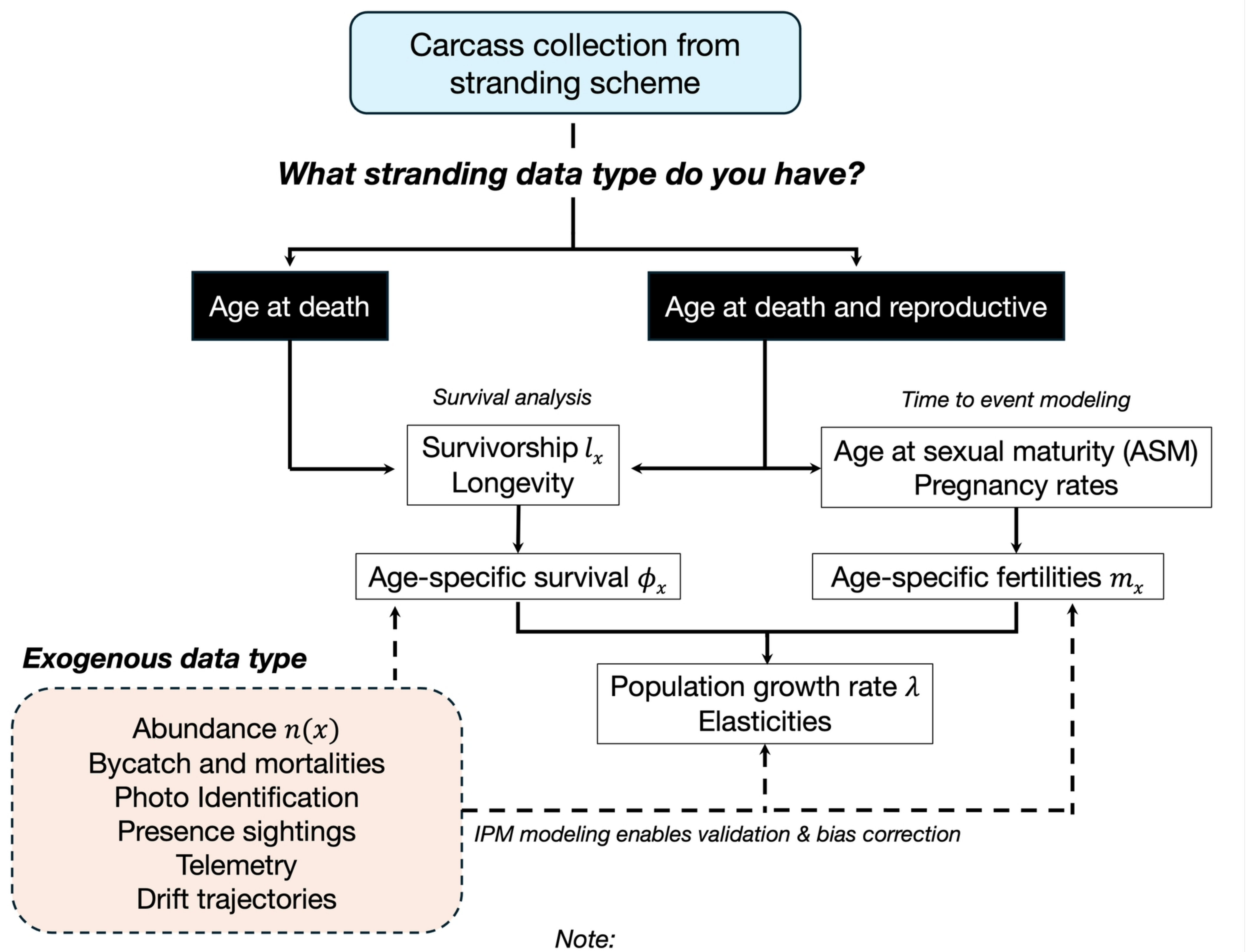

SELECTION PROCESS
BIAS SOURCES
Stage 1
$d(x) \propto n(x) \cdot q_x$
$r(x)$ = proportion of reproductively active
Death
Stage 2
Mortality by cause and location
Stage 3
Oceanographic drift and transport
Stage 4
Stranding and decomposition
Stage 5
Detection and reporting
Observed Strandings
$d_{\text{obs}}(x) \propto n(x) \cdot q_x \cdot \Pi p_i(x)$
$r_{\text{obs}}(x) \propto n(x) \cdot r(x) \cdot q_x \cdot \Pi p_i(x)$
Stage 6
Selected samples
Aged | Examined subset
$d_{\text{sample}}(x) \mid r_{\text{sample}}(x)$
Non stationarity Temporal variation $\Delta\mu(x,t)$
Age selective mortality causes $p_{\text{cause}}(x)$
Size dependant buoyancy $p_{\text{drift}}(x)$
Age-dependent decomposition and fine processes $p_{\text{strand}}(x)$
Size dependant detection $p_{\text{detect}}(x)$
Sampling protocol conditions $p_{\text{sample}}(x)$
AT SEA
ON LAND
Compounded selection bias progressively disstorts demographic inference



Note:
All demographic parameters can be stratified by sex, geographic zone, and/or time (multi-year series) to enable comparisons, trend detection, and region-specific inference

TITLE:

Stranding-Based Demographic Inference in Marine Mammals: Best Practices for Extracting Vital Rates Despite Compound Sampling Bias

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E.R. conceptualized the review and wrote it.

ABSTRACT

Strandings records provide the only demographic data source for many marine mammal species. Yet they may be heavily biased. Every carcass passes through sequential filtering: mortality cause, oceanographic drift, decomposition, detection, and sampling. Each stage distorts age-specific signals. This creates a fundamental paradox: strandings are essential yet appear unreliable for demographic inference. This review resolves the paradox through a systematic best practices. Strandings are formalized as a six-stage filtering cascade. Three complementary approaches extract reliable signals despite bias. Design-based protocols reduce sampling bias through stratified collection and standardized networks. Model-based temporal analyses detect relative demographic changes when detection remains constant. Integrated population models combine strandings with auxiliary data to correct bias. The review provides decision tools that formalize when and how demographic inference from strandings is defensible. Applications across harbor porpoises, common dolphins and manatees demonstrate that stranding-based monitoring reliably detects demographic changes. Three research priorities emerge from this review: quantifying age/stage-specific detection probabilities, incorporating spatial population structure, and parameterizing management strategy evaluation with stranding-derived demographic rates. When properly analyzed, strandings provide irreplaceable demographic surveillance for species inaccessible to other methods.

KEYWORDS:

conservation, demography, marine mammals, mortality, population dynamics, strandings, survival, vital rates

1 Introduction

Marine mammals are characterized by slow life history strategies: long generation times, delayed sexual maturity, low reproductive output, and high adult survival probabilities (Stearns, 1976; Fowler, 1988; Read and Hohn, 1995; Eberhardt, 2002). Quantified as vital rates (i.e. survival, fecundity, and fertility), these life history traits directly translate evolutionary strategies into population dynamics (Fowler, 1988; Gaillard et al., 1998; Tuljapurkar, 2013; Caswell, 2001). Vital rates combine to determine population growth rate (λ), the dominant eigenvalue of the population projection matrix, where $\lambda > 1$ indicates growth, $\lambda < 1$ decline, and $\lambda = 1$ stability (Caswell, 2001, 2019). Population growth rate in turn determines abundance trajectories: sustained changes in λ manifest as increasing or decreasing population size over time (Nicholson, 1954; Sibly and Hone, 2002). Environmental or anthropogenic pressures thus affect observable population abundance through their impacts on vital rates (Caswell, 2000, 2001; Coulson et al., 2001). For long-lived marine mammals, adult survival dominates this demographic link: small perturbations in adult survival probabilities can drive populations toward decline due to high elasticities of λ to this parameter (Heppell et al., 1998; Fujiwara and Caswell, 2001; Gerber and Heppell, 2004; Arso Civil et al., 2019; Caswell, 2019).

Abundance surveys alone may not detect population declines in time for effective conservation action (Gerrodette, 1987; Taylor et al., 2007; Caughley, 1994; Reed et al., 2002; Holmes et al., 2007; Authier et al., 2020). Statistical power to detect trends from abundance estimates remains dismally low: Taylor et al. (2007) found that 72% of precipitous declines (50% decrease in 15 years) in large whales, 90% in beaked whales, 100% for pinnipeds on ice, 55% for polar bears/sea otters and 78% in dolphins would go undetected given current monitoring effort. Similarly, Authier et al. (2020) demonstrated that even well-studied populations with short time-series and high coefficients of variation lack adequate power to detect declines before reaching critically low levels. Abundance estimates suffer from wide confidence intervals, infrequent survey intervals (often 6-11 years), low detection probabilities

(Hammond, 1995; Buckland and York, 2018; Hammond et al., 2021; Gilles et al., 2023), and long time lags between demographic change and detectable abundance shifts (Taylor et al., 2007; Gerrodette, 1987; Authier et al., 2020).

Vital rate monitoring offers a solution through earlier detection: demographic parameters change before abundance declines become statistically detectable (Caughley, 1994; Eberhardt, 2002; Holmes et al., 2007; Caswell, 2001; Fujiwara and Caswell, 2001; Morris and Doak, 2002; Sibly and Hone, 2002; Reed et al., 2002; De Silva and Leimgruber, 2019). This early warning capacity enables proactive rather than reactive management. Moreover, vital rate estimates identify which demographic processes drive population change—whether adult survival, juvenile recruitment, or fecundity—allowing targeted interventions rather than generic conservation measures (Gaillard et al., 1998; Heppell et al., 1998; Holmes et al., 2007; Authier et al., 2017).

The consequences of inadequate demographic monitoring can be catastrophic. The baiji (*Lipotes vexillifer*), declared functionally extinct in 2006, the Caribbean monk seal (*Neomonachus tropicalis*), extinct by 2008, the Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) with less than 500 individuals remaining, and the vaquita (*Phocoena sinus*), now functionally extinct with fewer than 10 individuals remaining, all suffered decades of demographic decline masked by persistence of remnant individuals (Turvey et al., 2007; McClenachan and Cooper, 2008; Huang et al., 2020; Rojas-Bracho et al., 2022). More recently, North Atlantic right whales (*Eubalaena glacialis*) provided clear demographic warnings (declining calving rates, increased calving intervals, elevated mortality from vessel strikes and entanglements) years before abundance fell below 350 individuals, yet insufficient management response has driven the species toward extinction (Pettis et al., 2021; Christiansen et al., 2020; Meyer-Gutbrod et al., 2021). Without robust demographic monitoring and timely intervention, even iconic species slip toward extinction

(Gerrodette, 1987; Caughley, 1994; Morris and Doak, 2002).

For many marine mammal species, strandings provide the only available demographic data source. This review demonstrates that despite recognized biases, modern analytical frameworks can extract reliable demographic signals from stranded carcasses. First, it traces the historical trajectory from early cross-sectional life tables through the longitudinal capture-recapture revolution, establishing why stranding data remain the only demographic data source for most marine mammal species despite recognized biases (Section 2). Second, it formalizes the sequential filtering process through a novel six-stage cascade (mortality, cause/location selection, drift, decomposition, detection, sampling) that identifies where age-specific biases enter the demographic inference and how they compound multiplicatively (Section 3). Third, it presents a set of best practices that systematically matches research questions with defensible analytical approaches by evaluating available data across four dimensions: biological measurements (age, reproductive status, cause of death), stratification structure (temporal series, spatial regions, individual covariates), sample size adequacy, and auxiliary data availability (Section 4). Examples from harbor porpoises, common dolphins and manatees demonstrate how design-based and model-based with and without auxiliary data enable detection of demographic change. Finally, it identifies three research priorities (quantifying detection probabilities, incorporating spatial population structure, and advancing simulation-based management tools) that will strengthen stranding networks as demographic surveillance systems and enable proactive management tools (Section 5). This review resolves the paradox of extracting reliable demographic signals from biased stranding data, providing the first comprehensive set of best practices of when and how strandings inform vital rate estimation through practical decision tools.

Box 1: Key Demographic Terms and Notation

CORE DEMOGRAPHIC CONCEPTS

- **Vital rates**: Survival, fecundity, and recruitment rates determining population dynamics
- **Life table**: Age-specific schedule of mortality and survival probabilities
- **Fecundity schedule**: Age-specific reproductive output across lifespan
- **Stable age distribution**: Population age structure that remains proportionally constant over time
- **Elasticity**: Proportional sensitivity of population growth rate to parameter changes
- **Cross-sectional inference**: Estimating vital rates from a snapshot of carcasses
- **Longitudinal inference**: Estimating vital rates from repeated observations of the same individual
- **Abundance**: Total population size summed across all age classes
- **Recruitment**: Number of new individuals entering the population per time unit

LIFE HISTORY PARAMETERS

- **Age at sexual maturity (ASM)**: Age when reproductive capability is attained
- **Maximum longevity**: Oldest recorded age at death in a population
- **Median lifespan**: Age at which 50% of a cohort has died
- **Gestation length**: Duration of pregnancy from conception to birth
- **Calving interval**: Time between successive births for an individual female

NOTATIONS

- λ: Population growth rate (dominant eigenvalue of projection matrix)
- ϕ_x: Age-specific survival probability (surviving from age x to $x + 1$; $\phi_x = 1 - q_x$)
- q_x: Age-specific probability of death (discrete mortality)
- l_x: Survivorship to age x (proportion of cohort surviving)
- μ_x: Age-specific instantaneous mortality rate (hazard rate; $\mu(x) = -\frac{d[\ln(l_x)]}{dx}$)
- m_x: Age-specific fertilities (mean offspring produced at age x)
- $r(x)$: Proportion reproductively active at age x
- e_0: Life expectancy at birth
- T: Generation time (mean age of reproduction)
- $n(x)$: Living population size at age x
- $d(x)$: True number of deaths at age x in the population
- $d_{\text{obs}}(x)$: Observed number of strandings at age x
- $r_{\text{obs}}(x)$: Observed reproductively active individuals at age x among strandings

2 Historical Context of Demographic Inference in Marine Mammals

Demographic inference for marine mammals has undergone two major methodological eras. Cross-sectional approaches dominated for over a century, extracting vital rates from carcasses (from hunting and standing) despite ackowledged sampling biases. Longitudinal capture-recapture methods revolutionized the field by separating mortality from detection, but remain feasible not for all species. For many marine mammals, systematic stranding networks now represent the only viable source of demographic data.

2.1 Cross-Sectional Foundations (1820s–1980s)

Cross-sectional demographic analysis—inferring vital rates from age-at-death distributions and reproductive status at death—emerged in the early 19th century as a foundational approach for constructing life tables and fecundity schedules (Gompertz, 1825). Caughley (1966) formalized the theoretical framework that remains foundational today, establishing that observed mortality and reproductive patterns directly reflect population age structure when four key assumptions hold: stable age distribution, time-invariant vital rates, representative age sampling, and accurate age determination. Under these conditions, age-at-death distributions yield survivorship curves (l_x), from which age-specific survival probabilities (ϕ_x) are derived. Reproductive examination establishes age at sexual maturity and pregnancy rates, which combine to provide age-specific fertility schedules (m_x). Together, survival (ϕ_x) and fertility (m_x) parameterize population projection matrices, enabling estimation of population growth rate (λ).

Systematic application to marine mammals emerged through mid-20th century commercial whaling, where industrial operations routinely collected biological samples enabling age determination from teeth, ear plugs, or baleen, and reproductive assessment from gonadal examination (Laws, 1953, 1961). Chapman (1964) pioneered actuarial methods for whale catch data, revealing fundamental cetacean life history patterns: elevated juvenile mortality, relatively constant adult survival, age-specific fecundity, and senescent declines (i.e. U-shaped mortality and hazard rate curce : Reed, 2011). Similar approaches applied to pinniped harvest programs provided basic demographic parameters and life history parameters for seal populations (Sergeant, 1973; Fowler, 1984). As commercial whaling declined through the 1970s–1980s, stranding records emerged as alternative data sources (Gulland et al., 2025), particularly for small cetaceans vulnerable to fishery bycatch but rarely taken in directed harvests (Perrin et al., 1994; Jefferson and Curry, 1994). Early applications followed established protocols, constructing survivorship curves, fecundity schedules and life tables from stranded carcasses (Hohn et al., 1989; Perrin and Reilly, 1984; Barlow and Boveng, 1991; Stolen and Barlow, 2003). However, accumulating evidence revealed intractable biases: systematic underrepresentation of neonates due to rapid decomposition and size-dependent detection, age-selective stranding probabilities varying by cause and location of death, violations of stationarity assumptions, and heterogeneous recovery rates across regions (Barlow and Boveng, 1991; Stolen and Barlow, 2003). Unlike whaling data where biases could be partially characterized through fishery statistics, stranding processes operated through complex, poorly quantified pathways where true mortalities could not be disentangled from sampling artifacts. By the 1990s, confidence in stranding-based vital rate estimation had eroded substantially, and their use for rigorous demographic inference declined as the field recognized the confounding between age-specific mortality and detection probabilities.

2.2 The Longitudinal Revolution (1980s–2000s)

Capture-mark-recapture (CMR) methods, developed in terrestrial and avian ecology (Cormack, 1964; Jolly, 1965; Seber, 1965; Pollock, 1982 ; or thereafter CR for capture-recatpure in the case of marine mammals), revolutionized demographic inference by estimating vital rates from repeated observations of individually identifiable animals over time (CMR uses artifical marks, CR uses natural marks). The Cormack-Jolly-Seber (CJS) framework (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton et al., 1992) provided the foundational approach: rather than assuming all deaths are observed, CMR explicitly models detection as a stochastic process with estimable probability, separating true survival from sampling artifacts through patterns of individual re-encounters. This directly addressed the confounding bias between mortality and detection that plagued cross-sectional inference. CMR requires that marked individuals are representative of the population, marks are permanent and do not affect survival or detectability, recapture probabilities are equal or measurable, and emigration can be distinguished from mortality (Lebreton et al., 1992). By the 1990s, CMR had become the gold standard for demographic inference across taxa, yielding direct estimates of age-specific survival (ϕ_x), breeding probability (ψ_x), breeding success (ρ_x), and fertilities (m_x) with quantified precision, enabling accurate estimation of population growth rate (λ) and rigorous hypothesis testing impossible from cross-sectional data.

Photo-identification techniques, which emerged in the late 1970s (Würsig and Würsig, 1977), enabled the application of CR methods to marine mammals by using natural markings—such as dorsal fin notches, fluke patterns, scarring, and pigmentation—for reliable individual recognition across years or decades. While telemetry can also be used for longitudinal monitoring (McConnell et al., 2004), it is still considered inefficient for inferring demographic rates (Booth et al., 2020). Landmark studies demonstrated the transformative power of photo-ID approaches: Bigg et al. (1990) revealed the matrilineal structure and precise vital rates of killer whales, while Fujiwara and Caswell (2001) parameterized population viability models for southern right whales using decades of photo-identification data. The Sarasota Bay bottlenose dolphin photo-ID program, established in the 1970s (Wells and Scott, 2000), became one of the reference model systems for cetacean demography and life history through CR (Wells and Scott, 1990; Wells, 2009, 2013). Methodological extensions subsequently expanded CR capabilities, with as examples: multistate models (Arnason, 1973; Nichols and

Kendall, 1992) enabled estimation of transitions between demographic states; robust design (Pollock, 1982) improved precision; and Bayesian frameworks (Wade, 2000) accommodated sparse data while propagating uncertainty. Recent applications have quantified immigration as a demographic driver (Tenan et al., 2023), revealed kinship effects on survival and post-reproductive lifespans (Croft et al., 2017; Nattrass et al., 2019), and detected fishery impacts on demography and social structure (Jordaan et al., 2023). Despite these advances, CR remains logistically infeasible for most marine mammal species.

2.3 Strandings as the Primary Demographic Data Source

While CMR (and CR) methods have revolutionized vital rate inference for accessible populations with identifiable individuals, many marine mammal species (particularly oceanic delphinids) remain logistically unfeasible to study using these approaches (Urian et al., 2015; Hammond et al., 2021; Hupman et al., 2018; see Table 1 for a functional group assessment). Oceanic delphinids lack individually distinctive dorsal fin patterns, or in some cases, lack dorsal fins entirely (Weinrich et al., 2001; Hupman et al., 2018), though emerging methodologies are beginning to enable photo-ID of poorly marked cetaceans (Elliser et al., 2022). These species also exhibit very low recapture probabilities, and the latest deep-learning approaches for photo-ID continue to struggle with low image quality, poorly pigmented animals, and unusual markings (Patton et al., 2023). Similarly, harbor porpoises are notoriously difficult to monitor through CR programs (Gaskin and Watson, 1985; Koopman and Gaskin, 1994; Baird, 2003), although recent studies have successfully used CR to assess site fidelity (Elliser et al., 2018, 2025). For beaked whales, detection probabilities are so low that vital rate inference from CR remains infeasible to date (New et al., 2013; Chiquet et al., 2015; Hooker et al., 2019).

For these species, systematic stranding networks may represent the only viable source of demographic data, from which it is possible to infer vital rates. Coordinated programs now document mortality and stranding patterns with standardized protocols, yielding multi-decadal databases of age, sex, reproductive status, body condition, and cause of death (Moore et al., 2020; Wilkin et al., 2017; Authier et al., 2014; IJsseldijk et al., 2018).

Table 1: **Demographic Parameters Obtainable by Functional Group**

Functional Group	**Available demographic data source**	**Monitored demographic quantities**	**Key Study Examples**
Cetaceans			
Coastal small cetaceans (e.g. harbor porpoise, finless porpoise, vaquita)	CR: Limited; Strandings: High	Age distribution; Reproductive schedule; Survivorship; Hierarchical survivorship; Temporal survivorship trends; Site fidelity	Read and Gaskin (1990); Hohn et al. (1996); Rouby et al. (2021); IJsseldijk et al. (2020a, 2021); Rouby et al. (2024); Elliser et al. (2018, 2025); Murphy et al. (2015); Kesselring et al. (2017)
Offshore dolphins (e.g. common, striped, spinner)	CR: Limited; Strandings: High	Age distribution; Reproductive schedule; Life tables; Survivorship; Population growth rate (absolute & relative); Temporal survivorship trends; Cause-specific mortality	Barlow (1984); Barlow and Boveng (1991); Calzada et al. (1997); Mannocci et al. (2012); Guarino et al. (2021); Roca-Monge et al. (2022); Rouby et al. (2025)

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Functional Group	**Available demographic data source**	**Monitored demographic quantities**	**Key Study Examples**
Inshore dolphins with photo-ID (e.g. bottlenose, killer whales - resident, common dolphin - resident)	CR: Yes (some pops); Strandings: Moderate	Age-specific survival; Fecundity; Recruitment; Population growth rate; Cause-specific mortality; Health indices; Population viability	Wells (2009); Bigg et al. (1990); Elliser et al. (2022); Nelson et al. (2024); Arso Civil et al. (2019); Williams et al. (2024)
Social large odontocetes (e.g. pilot whales, false killer whales, Risso's dolphins)	CR: Yes (some pops); Strandings: Moderate to High Huntings: Low to high	Age distribution; Survivorship; Life tables; Mortality schedules; Age at sexual maturity; Maximum longevity; Population-specific vital rates (CR populations); Mass-stranding demography	Kasuya and Matsui (1984); Bloch et al. (1996); Baird and Gorgone (2005); Hartman et al. (2016); Renò et al. (2019); Betty et al. (2023)
Deep-diving large odontocetes (e.g. beaked whales, sperm whales)	CR: Yes for some species; Strandings: Low to Moderate	Age distribution; Growth patterns; Age at sexual maturity; Maximum longevity; Life history parameters; Cause-specific mortality	Evans and Hindell (2004); D'amico et al. (2009); New et al. (2013); Chiquet et al. (2015); Hooker et al. (2019); Moore et al. (2018)

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Table 1 continued from previous page

Functional Group	Available demographic data source	Monitored demographic quantities	Key Study Examples
Large mysticetes with photo-ID (e.g. humpback, right, gray whales)	CR: Yes (some species); Strandings: Moderate	Age-specific survival; Fecundity; Calving intervals; Population growth rate; Body condition trends; Cause-specific mortality; Connectivity	Fujiwara and Caswell (2001); Moore et al. (2020); Christiansen et al. (2020); Meyer-Gutbrod et al. (2021); Pirotta et al. (2025)
Large mysticetes without photo-ID (e.g. minke, fin, sei, blue whales)	CR: Very limited; Strandings: Low to Moderate	Age distribution; Growth patterns; Age at sexual maturity; Reproductive parameters; Life tables; Cause-specific mortality (opportunistic)	Laws (1961); Lockyer (1993); Matthews et al. (2001); Arrigoni et al. (2011)
Pinnipeds			
Phocid seals at accessible colonies (e.g. harbor, gray, elephant seals)	CR and CMR/Tagging: Yes (colonies); Strandings: High	Age-specific survival; Fecundity; Recruitment; Population growth rate; Offshore mortality; Disease prevalence; IPM-derived vital rates	Boyd et al. (1995); Heppell et al. (1998); Pistorius et al. (2011); Rotella et al. (2012); Mosnier et al. (2023); Carroll et al. (2024); McCarthy et al. (2025)

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Table 1 continued from previous page

Functional Group	**Available demographic data source**	**Monitored demographic quantities**	**Key Study Examples**
Phocid seals, dispersed/ice-breeding (e.g. harp, hooded, ringed seals)	CR: Limited; Strandings: Moderate Huntings: Moderate	Age distribution; Reproductive parameters; Juvenile dispersal mortality; Harvest-based vital rates; Climate impact indices	Sergeant (1973); Roff and Bowen (1983); Fowler (1984); Reimer et al. (2019); Andersen et al. (2021); Nater et al. (2024)
Otariid seals (e.g. sea lions, fur seals)	CR and CMR/Tagging: Yes (colonies); Strandings: Moderate to High	Age structure; Age-specific survival; Fecundity; Pup survival; Recruitment; Cause-specific mortality; Elasticities; Population Viability	Holmes and York (2003); Holmes et al. (2007); Gerber and Heppell (2004); Heppell et al. (1998); Maniscalco et al. (2015); Harting et al. (2021); Hastings et al. (2023); Warlick et al. (2023)
Other Marine Mammals			
Sirenians (manatees, dugongs)	CR: Partial (photo-ID); Strandings: High	Age-specific survival; Fecundity; Population growth rate; Cause-specific mortality	Eberhardt and O'shea (1995); Langtimm et al. (1998, 2004); Runge et al. (2004); Hostetler et al. (2021)

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Table 1 continued from previous page

Functional Group	**Available demographic data source**	**Monitored demographic quantities**	**Key Study Examples**
Marine mustelids (sea otters)	CR: Partial (tags); Strandings: Low	Cause-specific mortality; Mortality sensitivity; Age distribution; Reproductive parameters ; Pup survival	Siniff and Ralls (1991); Bodkin et al. (2000); Monnett and Rotterman (2000); Monson et al. (2000); Estes et al. (2003); Gerber et al. (2004); Burek Huntington et al. (2021); Tinker et al. (2021)
Arctic specialists (e.g. walrus, narwhal, polar bears)	CR: Yes (some species); Strandings: Low Huntings: High	Age distribution; Reproductive parameters; Survival (harvest/telemetry-based); Connectivity/migration ; Population viability	Regehr et al. (2018); Bohart et al. (2021); Regehr et al. (2021); Taylor et al. (2021); Biddlecombe and Watt (2022); Braund et al. (2022); Garde et al. (2022); Breed et al. (2024); Rode et al. (2024)

Notes: CR = Capture-recapture (photo-ID). ”High” stranding data indicates well-established networks with consistent coverage. ”Limited” CR feasibility indicates method works for specific applications (e.g., site fidelity) but not population-wide vital rates.

3 The Stranding Pathway: From Death to Demographic Data

Stranding records are not random samples of population mortality. Every carcass passes through sequential filtering stages (from death at sea through drift, decomposition, detection, and selective sampling) each introducing age-specific and condition-specific biases that compound multiplicatively. Understanding this cascade of sampling processes is essential for rigorous demographic inference.

3.1 The Stranding Process as Sequential Filtering

Classical life table construction from age-at-death data requires four assumptions (Caughley, 1966): (1) stable age distribution, (2) time-invariant mortality, (3) random age sampling, and (4) accurate aging. When these assumptions hold, observed age distributions directly inform vital rates (Caughley, 1977). However, stranding data systematically introduce biases at multiple sequential stages between death and dataset inclusion, resulting in compounded distortion of the true mortality signal (see Figure 1).

The stranding of dead marine mammals is inherently a multi-stage process (Peltier et al., 2012, 2013, 2016; Deslias et al., 2024). Peltier et al. 2012 first formalized this process as: $N_{stranded\,cetaceans} = p_{buoyant} \times p_{stranding} \times p_{discovery} \times N_{dead\,at\,sea}$, where $p_{buoyant}$ represents the probability that a carcass is positively buoyant and can drift, $p_{stranding}$ is the probability that a drifting carcass reaches the coast, and $p_{discovery}$ is the probability that a stranded cetacean is discovered and reported to authorities. This review expands this definition to a demographic context, where marine mammal sampling through strandings passes through six filtering stages, each introducing age-specific and condition-specific sampling biases.

Stage 1: Mortality in the Living Population. The number of deaths at age x is proportional to $d(x) \propto n(x) \cdot q_x$, where $n(x)$ is population size and q_x is the age-specific probability of death (Caughley, 1966), assuming stable demography and constant vital rates. Non-stable age distributions—in growing, declining, or recovering populations—cause declining populations to appear to have inflated mortality and expanding populations to show artificially high survival (Caughley, 1977). Temporal variation in mortality from environmental change or anthropogenic pressures yields survival estimates representing unknown historical mixtures rather than current rates (Caughley, 1977; Caswell, 2001). These violations bias inference *before* any stranding-specific processes occur.

Stage 2: Differential Mortality by Cause and Location. The stranding pathway is already selective before any carcass enters the water: neonates dying nearshore from nutritional stress strand at vastly higher rates than healthy adults dying offshore (IJsseldijk et al., 2020a); adults killed in fisheries may be discarded at sea, never reaching shore (Peltier et al., 2016); senescent individuals dying far offshore may sink in deep water; sick animals may move coastward, inflating their stranding probability. The age distribution of *potentially strandable* carcasses thus diverges from true population mortality before oceanographic processes even begin.

Stage 3: Drift and Oceanographic Transport. Buoyant carcasses must drift ashore, with probability depending on distance from shore, currents, winds, carcass buoyancy, and coastline configuration, factors that correlate systematically with age and body condition. Juveniles drift differently than adults due to size-dependent buoyancy; carcasses with thick blubber remain buoyant longer than emaciated ones; seasonal oceanographic variation interacts with seasonal age structure of mortality. Peltier et al. (2013) demonstrated through drift modeling that even under spatially uniform mortality, stranding distributions become highly heterogeneous due to physical transport processes alone, revealing biological signals only after explicit oceanographic correction.

Stage 4: Stranding and Decomposition. Carcasses reaching shore continue to decompose (already started at sea) at age-dependent rates, with neonates and juveniles decomposing rapidly (hours to days) and causing systematic underrepresentation (Moore et al., 2021). Summer strandings decompose faster than winter ones, beach substrate and scavenger access affect persistence, and this detection window varies systematically with carcass size and condition, further distorting observed age distributions independent of actual mortality patterns.

Stage 5: Detection and Reporting. Detection probability depends on coastline accessibility, human density, monitoring effort, carcass size, and decomposition state (Peltier et al., 2016; Authier et al., 2014). Larger individuals are more conspicuous than small ones, and temporal variation in monitoring effort confounds trend detection: apparent stranding increases may reflect improved reporting infrastructure rather than elevated mortality (ten Doeschate et al., 2018). IJsseldijk et al. (2021) demonstrated that integrating near-shore sightings with strandings can distinguish abundance-driven from mortality-driven stranding rates—revealing genuine unusual mortality events after accounting for local population density.

Stage 6: Sampling and Necropsy Selection. Even after detection, not all stranded carcasses enter demographic datasets. Sampling protocols vary by network objectives and resources: health surveillance programs prioritize fresh carcasses with intact organs for pathological examination (IJsseldijk et al., 2018), systematically excluding decomposed individuals; research-focused networks may target specific age classes or species; logistical constraints (accessibility, storage capacity, funding) force selective sampling based on carcass condition, size, or species rarity (Simeone and Moore, 2018; Gulland et al., 2025). This final filter ($p_{\text{sample}}(x)$) creates systematic bias often overlooked in demographic analyses: opportunistic sampling toward well-preserved carcasses underrepresents rapidly decomposing juveniles and offshore mortality, while condition-dependent selection can artificially inflate apparent health or survival of sampled individuals. The selected sample examined for age determination (Read et al., 2018) and reproductive status (Murphy et al., 2015; Kesselring et al., 2017) thus represents a non-random subset of detected strandings, further distorting the demographic signal before any analysis begins.

3.2 The Compounded Bias Problem

This cascade can be formalized mathematically to clarify how biases compound. The observed stranding data reflect true actual demographic processes multiplied by all detection probabilities::

$$d_{\text{obs}}(x) \propto n(x) \cdot q_x \cdot \prod_i p_i(x) \tag{1}$$

$$r_{\text{obs}}(x) \propto n(x) \cdot r(x) \cdot q_x \cdot \prod_i p_i(x) \tag{2}$$

where $d_{\text{obs}}(x)$ is the observed number of strandings at age x, $r_{\text{obs}}(x)$ is the observed number of reproductively active individuals at age x among strandings, $n(x)$ is the living population size at age x, q_x is the true age-specific mortality probability, $r(x)$ is the true age-specific proportion reproductively active in the population, and $\prod_i p_i(x) = p_{\text{cause}}(x) \cdot p_{\text{drift}}(x) \cdot p_{\text{strand}}(x) \cdot p_{\text{detect}}(x) \cdot p_{\text{sample}}(x)$ represents the compound age-specific probability of being observed and sampled given death has occurred.

Without independent estimates of these sampling probabilities, age-specific mortality probability q_x, age-specific survival probability ϕ_x and the proportion of reproductive individuals $r(x)$ cannot be disentangled from detection processes: the central statistical challenge of stranding-based demography (See Box 2 for a concrete example). Age classes that appear over-represented in stranding data may reflect genuinely elevated mortality, higher stranding/detection probability, or both; conversely, under-represented age classes (particularly neonates) may experience substantial mortality that remains invisible in stranding records. Similarly, observed reproductive patterns may reflect true population fecundity or systematic biases in which reproductive states are sampled. Superimposed on these sampling biases, age determination error from methodological imprecision or biological variation further blurs age-class boundaries and attenuates survival gradients (Hohn et al., 1989; Stolen and Barlow, 2003).

Box 2: Example of compounding biases in stranding data

SCENARIO: Consider a dolphin population experiencing fishery bycatch mortality. Adult dolphins (ages 5–15) suffer elevated bycatch mortality nearshore, yielding genuinely high q_x for these age classes. However, the compound sampling process creates systematic distortion at every stage:

STAGE-SPECIFIC BIASES:

- **Stage 2 ($p_{\textbf{cause}}$):** Discarded bycatch carcasses may be retained or thrown overboard depending on fishery regulations and observer presence
- **Stage 3 ($p_{\textbf{drift}}$):** Small juveniles and large adults drift differently due to size-dependent buoyancy
- **Stage 4 ($p_{\textbf{strand}}$):** Summer bycatch events in warm waters lead to rapid decomposition compared to winter strandings
- **Stage 5 ($p_{\textbf{detect}}$):** Heavily fished regions with high human density detect more carcasses than remote coasts
- **Stage 6 ($p_{\textbf{sample}}$):** Field teams prioritize fresh, well-preserved carcasses for necropsy, systematically excluding decomposed individuals

RESULTING CONFOUNDS: The observed age distribution of examined strandings reflects: (1) genuine elevation of adult mortality from bycatch, confounded with (2) higher detection of nearshore adult mortality, (3) size-selective drift and decomposition, (4) spatially heterogeneous monitoring effort, and (5) condition-dependent sampling.

Key message: Disentangling demographic signal from bias artifact requires either independent quantification of each $p_i(x)$ term (rarely possible) or analytical frameworks that circumvent absolute rate estimation by focusing on relative temporal changes or spatial comparisons where biases remain constant (Rouby et al., 2024, 2025).

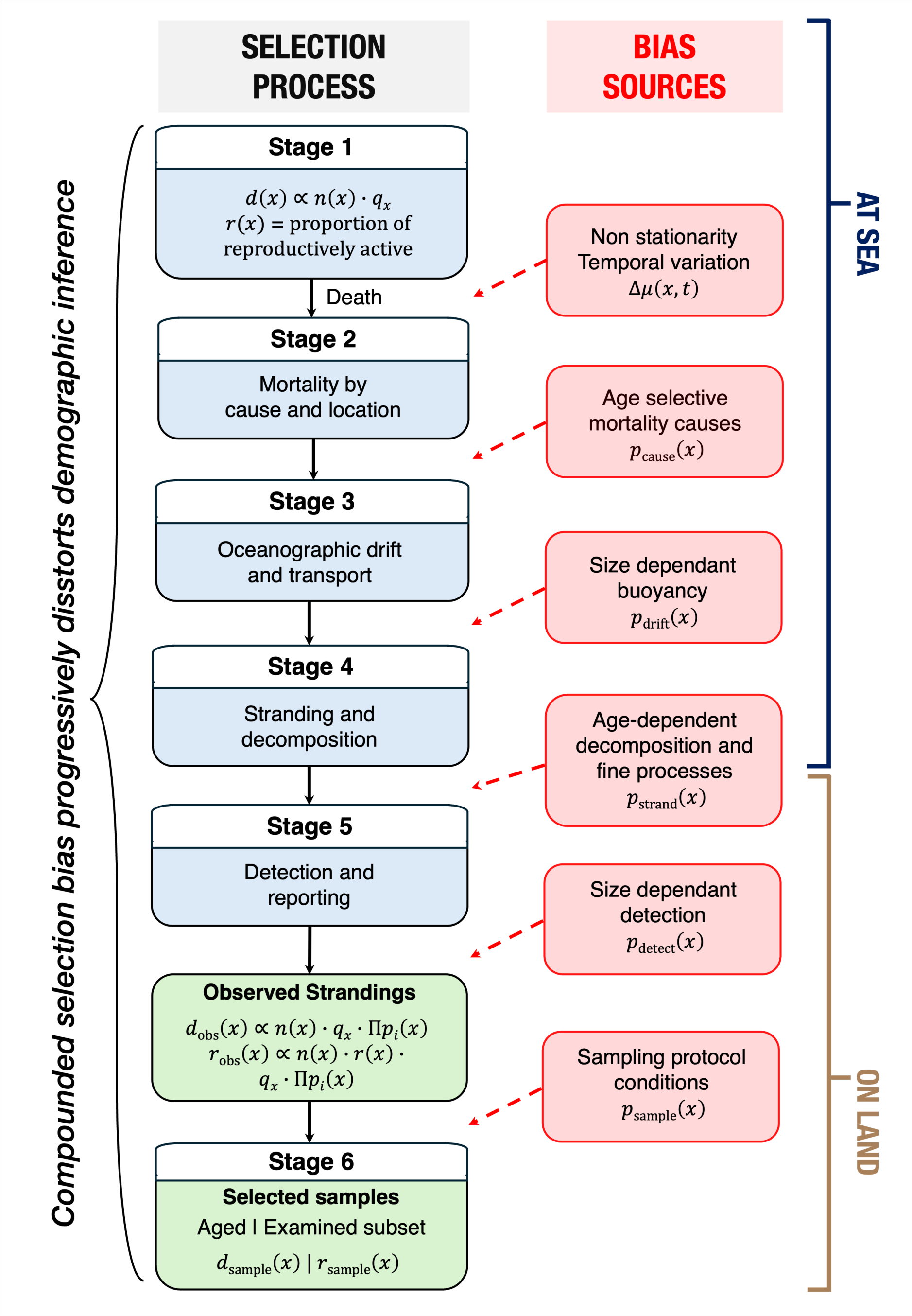

Figure 1: **The stranding pathway cascade and sources of bias in demographic inference.** Marine mammal deaths pass through six sequential filtering stages (left, blue boxes). Stage 1 shows true mortality ($d(x) \propto n(x) \cdot q_x$) and proportion of reproductively active individuals ($r(x)$) in the living population. Observed strandings (green box) include compound sampling bias: $d_{\text{obs}}(x) \propto n(x) \cdot q_x \cdot \prod p_i(x)$, where $\prod p_i(x)$ is the product of all age-specific detection probabilities. Each bias source (right, red boxes) introduces age-specific sampling probabilities (p_{cause}, p_{drift}, p_{strand}, p_{detect}, p_{sample}) that compound multiplicatively. Stage 6 shows the final selected sample examined for demographic analysis.

4 Best Practicesfor Demographic Inference from Strandings

Section 3 formalized the compound bias problem: observed strandings reflect true demographic processes multiplied by age-specific detection probabilities across six sequential stages (Equations 1–2). Without independent estimates of $\prod p_i(x) = p_{\text{cause}}(x) \cdot p_{\text{drift}}(x) \cdot p_{\text{strand}}(x) \cdot p_{\text{detect}}(x) \cdot p_{\text{sample}}(x)$, absolute vital rates cannot be reliably estimated from stranding records alone. However, three complementary strategies enable extraction of meaningful demographic signals despite these biases: design-based approaches reduce selection bias at the final sampling stage; model-based approaches using carcasses alone detect relative temporal changes when biases remain constant; and model-based approaches combining strandings with auxiliary data to implicitely remove bias terms. Together, these form a coherent set of best practices for demographic inference that respects inherent limitations while maximizing information content. **This set answers a fundamental question: given the research objective and available stranding data, characterized by data type (age, reproduction, covariates), stratification (temporal, spatial, individual), and sample size, which demographic parameters can be reliably estimated, and which analytical approach should be used?** This section presents each approach, demonstrates successful applications, and provides decision tools to match research questions with appropriate analytical methods.

4.1 Design-Based: Reducing Stage 6 Sampling Bias

Design-based methods directly address the final filtering stage—selective sampling and necropsy ($p_{\text{sample}}(x)$) through systematic protocols and stratified sampling. While they cannot eliminate biases inherent to Stages 1–5 (mortality processes, oceanographic drift, decomposition, and detection), standardizing sample selection substantially improves demographic inference by ensuring examined carcasses represent the broader stranding distribution rather than opportunistically selected subsets.

Stratified random sampling exemplifies this approach: by systematically sampling across decomposition states, locations, and time periods, researchers ensure representative age coverage rather than preferential selection of well-preserved individuals (Siniff and Skoog, 1964; Rouby et al., 2025). For instance, explicit stratification protocols that mandate inclusion of decomposed carcasses proportional to their detection frequencies directly correct the bias toward fresh specimens, thereby improving estimates of life history parameters and vital rates.

Beyond sample selection, standardized necropsy protocols reduce measurement variance in critical demographic assessments. Consistent procedures for age determination from tooth or ear plug reading and reproductive status assessment from gonadal histology improve precision of age-at-death, age at sexual maturity and fecundity estimates (Geraci and Lounsbury, 1999; Hohn et al., 1989).

Coordinated multi-regional networks implementing consistent sampling schemes enable spatial demographic comparisons while controlling for regional detection heterogeneity. IJsseldijk et al. (2018) demonstrated that standardized protocols across European stranding networks revealed spatiotemporal mortality patterns in harbour porpoises that informed population structure and anthropogenic impact assessment. Quantified monitoring effort—documenting search intensity, beach coverage, and temporal consistency—enables baseline modeling that distinguishes reporting artifacts from genuine mortality changes. ten Doeschate et al. (2018) showed that effort-corrected stranding rates provide reliable anomaly detection, essential for using strandings as mortality indices in demographic models.

Design-based improvements apply universally: even when absolute vital rates remain biased by Stages 1–5, reducing Stage 6 bias enhances reliability of life history parameters (maximum longevity, median lifespan, growth curves) and increases precision of all downstream demographic estimates. These improvements form the foundation upon which model-based approaches build.

4.2 Model-Based from carcasses only: Detecting Relative Change Despite Absolute Bias

Model-based approaches, focusing on hierarchical patterns, accept that absolute vital rates may remain biased by the compound detection process but focus on detecting *relative* changes over time or *comparative* patterns across groups where biases cancel or remain constant. Building on Equations 1–2, consider a time series of strandings from years $t_1, t_2, \ldots, t_{10}$ spanning a decade. At any time point t, observed strandings at age x follow:

$$d_{\text{obs}}(x,t) \propto n(x,t) \cdot q_x(t) \cdot \prod p_i(x,t) \tag{3}$$

If the compound detection probability remains constant over time—that is, $\prod p_i(x,t_1) = \prod p_i(x,t_2) = \cdots = \prod p_i(x,t_{10}) = \prod p_i(x)$ due to consistent sampling protocols, stable oceanographic conditions, and unchanged monitoring effort—then the ratio of observed strandings between any two time points becomes:

$$\frac{d_{\text{obs}}(x,t_2)}{d_{\text{obs}}(x,t_1)} = \frac{n(x,t_2) \cdot q_x(t_2) \cdot \prod p_i(x)}{n(x,t_1) \cdot q_x(t_1) \cdot \prod p_i(x)} = \frac{n(x,t_2) \cdot q_x(t_2)}{n(x,t_1) \cdot q_x(t_1)} \tag{4}$$

The bias terms $\prod p_i(x)$ cancel exactly, leaving the ratio of observed strandings proportional to the ratio of true mortality scaled by population size. When analyzing survivorship curves constructed from age-at-death distributions, temporal changes in observed survival probabilities $\phi_x(t)$ directly reflect changes in true survival when $\prod p_i(x)$ remains stable, even though absolute survival estimates may be biased. Validation of this assumption requires case-specific analysis of monitoring effort (Authier et al., 2014), drift conditions (Peltier et al., 2012, 2016), patterns of human-induced mortalities (Peltier et al., 2013, 2021) and reporting infrastructure but cannot be prescribed universally.

Classical cross-sectional methods assumed time-invariant vital rates and relied on parametric survivorship models (Gompertz, Weibull, Siler bathtub curves; Mannocci et al., 2012) that may inadequately capture marine mammal mortality patterns (Siler, 1979; Heligman and Pollard, 1980). Modern frameworks employ flexible hazard functions—splines, generalized additive models, piecewise exponential distributions—that accommodate complex age-specific mortality without imposing restrictive parametric assumptions (Reed, 2011). Bayesian implementations (Rouby et al., 2021, 2024) provide natural frameworks for incorporating prior biological knowledge, propagating uncertainty through demographic calculations, and accommodating sparse data through hierarchical structures (Moore and Read, 2008a). Critically, Bayesian frameworks enable formal comparison of models with and without temporal trends, providing rigorous hypothesis testing for demographic change detection. Temporal trend detection from strandings age-at-death data remains an emerging analytical frontier, as demonstrated in the following application.

The Bay of Biscay common dolphin population provides a compelling demonstration of early warning detection from stranding-based survival trends. Despite substantial fishery bycatch mortality and no detectable abundance decline from surveys conducted in 1994, 2005, and 2016 (Hammond, 1995; Gilles et al., 2023), temporal analysis of 759 aged individuals from 2000–2017 strandings revealed a 7-year decline in median longevity over two decades (from 22.3 to 15.6 years; 95% credible interval for decline: 5.2–9.1 years), yielding an estimated 2.4% cumulative reduction in population growth rate (Rouby et al., 2025). The analysis combined design-based stratified random sampling to correct for sampling bias ($p_{\text{sample}}(x)$) with model-based temporal trend detection, while validating that the remaining detection probabilities ($\prod p_i(x)$) remained constant over the study period, allowing temporal changes in observed age distributions to be attributed to genuine demographic health deterioration.

Similar model-based frameworks apply to reproductive parameters. Flexible models (Weibull, generalized logistic) for age-at-sexual-maturity estimation implemented in Bayesian frameworks accommodate individual variation and measurement uncertainty better than classical logistic regression, improving precision of this critical life history parameter (Kesselring et al., 2017). Comparative analyses across sexes, regions, or time periods follow identical logic: if sampling protocols remain consistent, observed differences reflect biological variation rather than detection artifacts.

Model-based innovations transform stranding data from static life tables into dynamic demographic surveillance systems capable of detecting population deterioration before abundance impacts manifest. The approach requires: (1) adequate sample sizes (e.g. $n > 300$ for survivorship temporal trends, see Rouby et al., 2021 and Rouby et al., 2024; species-specific simulation recommended), (2) multi-year time series, (3) consistent sampling protocols to avoid $p_{\text{sample}}(x)$ introduction and (4) careful validation that detected changes to ensure stable $\prod p_i(x)$. So signals reflect demography rather than evolving detection processes.

4.3 Model-Based: Quantifying Compound Bias Through Auxiliary Data

Integrated population models (IPMs) offer the current most powerful tool for stranding-based demography by directly addressing the central statistical challenge: independent quantification of the compound bias terms $\prod p_i(x)$ from Equations 1–2. IPMs combine multiple data sources (e.g. abundance surveys, mark-recapture studies, bycatch observations, oceanographic models, and strandings) within a unified statistical framework that probabilistically constrains demographic parameters across complementary datasets (Besbeas et al., 2002; Schaub and Abadi, 2011; Zipkin and Saunders, 2018). By explicitly accounting for each source's uncertainty and bias structure while leveraging their collective strengths (Kéry and Schaub, 2012; Abadi et al., 2010).

When stranding data complement photo-identification (photo-ID) studies, the synergetic integration is particularly powerful. Strandings provide age-at-death, cause-specific mortality, body condition, and reproductive status: information unavailable from photo-ID sightings alone. Photo-ID provides survival estimates and detection probabilities that validate stranding-based parameters and correct for incomplete carcass recovery.

Hostetler et al. (2021) demonstrated this synergy for Florida manatees, combining aerial abundance surveys, systematic carcass recovery, and photo-ID histories to reconstruct 20-year population dynamics ($\lambda = 1.02$; 95% CI 1.01–1.03). The integrated population model estimated age-specific carcass recovery probabilities for the first time, revealing high detection for adults (97%; 90–100%) and subadults (95%; 87–98%) but substantially lower rates for calves (67%; 48–84%), and quantified how detection varied temporally, reaching lows of 29% for calves during mortality events. This integration proved critical for assessing the 2013 red tide event: while 353 manatee carcasses were documented, the IPM estimated true mortality at 331 deaths (217–466), demonstrating that even with high recovery effort, raw carcass counts captured most but not all mortality. Crucially, integration with photo-ID survival data revealed that detection probability varied systematically by mortality event type (lowest during red tides, highest during cold events), enabling correction for age-specific and event-specific detection biases that would otherwise confound mortality assessments. The model also estimated previously unknown juvenile survival probabilites, filled abundance gaps for non-survey years, and quantified the population-level impact of the red tide ($\lambda = 0.89$ in 2013), insights unattainable from any single data stream.

Integrated approaches like IPMs demand coordinated data collection and substantial analytical investment but yield demographic insights impossible from any single data source. Minimum requirements include: (1) at least two complementary data types (typically strandings + abundance or strandings + mark-recapture), (2) temporal overlap across datasets, (3) explicit models linking each data type to underlying demographic parameters, and (4) quantified uncertainty in bias terms. When these conditions are met, IPMs provide the methodological pathway for transforming stranding data from biased samples into rigorous demographic monitoring tools by explicitly estimating—rather than ignoring or assuming constant—the compound detection process.

4.4 Matching Research Questions to Analytical Methods

The three frameworks above (design-based, model-based using crcasses only and integrated model-based) address different aspects of the compound bias problem and support different types of demographic inference. Selecting the appropriate framework requires matching research questions with data characteristics, available auxiliary information, and acceptable levels of inference. Questions are organized in Table 2 by inferential requirements, key assumptions, major biases, and recommended approaches, with detailed guidance on parameters and key references for each question type. The structure reflects a fundamental reality: life history parameters remain defensible despite violations of classical assumptions, vital rates require careful validation, while temporal trends and comparisons can circumvent absolute bias through focus on relative changes. Users should identify their research question, assess whether available data meet the stated assumptions, and select analytical approaches accordingly. When assumptions are violated or biases cannot be adequately addressed, narrower questions may remain answerable under a set of reasonnable and explicitely stated assumptions.

Questions are grouped into five categories reflecting increasing complexity:

1. **Life history parameters** (maximum longevity, age at sexual maturity, gestation

length, growth patterns): Relatively robust to compound bias because they describe biological characteristics rather than population-level rates. Design-based approaches suffice for most applications.

2. **Vital rates** (age-specific survival, fecundity schedules): Require strong stationarity assumptions and are directly affected by all bias stages. Absolute estimation demands auxiliary data; relative comparisons across groups feasible with model-based methods under constant $\prod p_i(x)$.
3. **Population metrics** (population growth rate λ, generation time T): Compound multiple biased vital rate estimates, propagating uncertainty from each component. Model-based with auxiliary data essential unless inference focuses solely on direction of change.
4. **Temporal trends** (declining survival, changing longevity, early warning signals): Model-based approaches excel here because relative change detection circumvents absolute bias quantification. Requires consistent sampling protocols and adequate time series.
5. **Comparisons** (sex differences, regional variation, cause-specific patterns): Feasible when sampling protocols are comparable across comparison groups, allowing biases to cancel. Both model-based and design-based approaches applicable depending on question.
6. **Integrated approaches** (population viability analysis, demographic drivers): Leverage multiple data streams to validate parameters and quantify bias structure. Represent the frontier of stranding-based demography but require substantial data and analytical investment.

Table 2: **Research Questions, Methods, and Limitations in Stranding-Based Demographic Analysis**

Research Question	**Parameter**	**Key Assumptions**	**Major Biases**	**Reference examples**
Life History Parameters				
Longevity?	Max age at death	Representative old-age sampling	Old animals underrepresented	(George et al., 1999; Venuto et al., 2020; Breed et al., 2024; Rouby et al., 2025)
Mean/median lifespan?	Life expectancy (e_0)	Stationary age distribution	Age-selective stranding	(Betty et al., 2023)
Age at sexual maturity?	Age when 50% of the sample is maturen	Stranded females representative	Sick/injured may differ and age selection	(Read and Gaskin, 1990; Hohn et al., 1996; Kesselring et al., 2017; Roca-Monge et al., 2022)
Gestation length?	Pregnancy duration	Accurate fetal aging	Small samples; seasonal bias	(Perrin and Reilly, 1984; Barlow, 1984; Calzada et al., 1997)

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Research Question	**Parameter**	**Key Assumptions**	**Major Biases**	**Reference examples**
Growth patterns?	Length/mass at-age	Representative age-size sampling	Young classes undersampled	(Calzada et al., 1997; Evans and Hindell, 2004; Venuto et al., 2020; Guarino et al., 2021)
Vital Rates				
Age-specific survival?	ϕ_x	Stationarity; no age bias; accurate aging	Nonstationarity; differential detection	(Barlow and Boveng, 1991; Stolen and Barlow, 2003; Mannocci et al., 2012; Rouby et al., 2025)
Age-specific mortality?	q_x	Stationarity; no age bias; accurate aging	Nonstationarity; differential detection	(Heligman and Pollard, 1980; Barlow and Boveng, 1991; Stolen and Barlow, 2003; Moore and Read, 2008a; Betty et al., 2023)

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Research Question	**Parameter**	**Key Assumptions**	**Major Biases**	**Reference examples**
Survivorship curve?	l_x	Representative mortality across ages	Neonate undersampling	(Siler, 1979; Stolen and Barlow, 2003; Arrigoni et al., 2011; Reed, 2011; Mannocci et al., 2012; Saavedra, 2018; Betty et al., 2023; Rouby et al., 2021)
Mortality hazard?	μ_x	Constant hazard within age	Bathtub shape needs flexible models	(Reed, 2011; Rouby et al., 2021)
Age-specific fecundity?	m_x	Representative females	Stress-induced abortion	(Perrin and Reilly, 1984; Murphy et al., 2015; Kesselring et al., 2017)
Population Metrics				
Population growth?	λ (matrix model)	All vital rate assumptions valid	Compounds all biases	(Mannocci et al., 2012; Moore and Read, 2008a)
Generation time?	Mean age reproduction (T)	Stable age distribution	Biased if ASM/longevity biased	(Stolen and Barlow, 2003; Mannocci et al., 2012)

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Table 2 continued from previous page

Research Question	**Parameter**	**Key Assumptions**	**Major Biases**	**Reference examples**
Temporal Trends				
Survival declining?	Trend in ϕ_x	Constant detection over time	Effort/drift changes	(Rouby et al., 2024, 2025)
Longevity changing?	Trend in mean/max age	Consistent protocol; stratified design	Observer effort varies	(Rouby et al., 2024, 2025)
Early warning?	Relative vital rate change	Constant selection bias	Short series lack power	(Rouby et al., 2024, 2025)
Comparisons				
Sex differences?	Sex-specific ϕ_x or l_x	Sex bias constant over time	Differential offshore mortality	(Stolen and Barlow, 2003; Betty et al., 2023)
Regional differences?	Spatial vital rate variation	Comparable sampling effort	Drift varies by region	(IJsseldijk et al., 2018, 2020b)
Cause-specific mortality?	Mortality by cause	Accurate determination	Discards underdetected	(Peltier et al., 2016; Moore et al., 2021; Peltier et al., 2021)
Integrated Approaches				

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Table 2 continued from previous page

Research Question	**Parameter**	**Key Assumptions**	**Major Biases**	**Reference examples**
Population viability?	Multiple rates + λ	Integration with surveys/CMR	Reduced not eliminated	(Hostetler et al., 2021; Nelson et al., 2024)
Demographic drivers?	Limiting vital rate	IPM framework	Bias structure modeled	(Fujiwara and Caswell, 2001; Hostetler et al., 2021; Nelson et al., 2024)

Notes: This table summarizes key demographic questions addressable with stranding data, required assumptions, major sources of bias, and foundational references. ASM = Age at Sexual Maturity.

4.5 Practical Guide for Selecting Analytical Approaches

As a reminder, a common fundamental question arising when working with stranding data is: **given available samples and a specific research objective, which analytical approach is appropriate?** The answer depends on connecting research questions (Table 2) with data characteristics through a decision pathway that embodies a fundamental principle: extract maximum information from available data while respecting inherent constraints without over extrapolating. Rather than abandoning inference when ideal conditions are absent, the pathway guides adaptation of methods to answer narrower but still meaningful questions. This logic flows from biological measurements (age, reproduction, covariates) through analytical approaches to demographic parameters (l_x, ϕ_x, q_x, m_x, λ), as synthesized visually in Figure 2.

Step 1: Assess available data. Four data characteristics determine analytical possibilities:

- *Biological measurements*: Age-at-death enables survivorship curves (l_x) and age-specific survival probability (ϕ_x). Adding reproductive status enables fertilities (m_x). Combined, ϕ_x and q_x allow population growth rate (λ) estimation (Caswell, 2001).
- *Stratification structure*: Temporal series enable trend detection or time period comparison. Spatial stratification enables regional comparisons. Individual time-invariant covariates (i.e., zone, sex, cause of death) enable demographic partitioning.

- *Sample size*: Required sample sizes depend critically on species life history (generation time,longevity, age at maturity) and analytical objectives (detecting subtle vs. precipitous declines). Simulation studies tailored to each case (using known or assumed demographic parameters and realistic bias structures) provide defensible guidance for adequacy assessment.
- *Auxiliary data availability*: Abundance surveys, mark-recapture studies, bycatch observations, or drift models enable integrated approaches that validate and correct bias.

Step 2: Identify the research question. Table 2 organizes demographic questions by inferential requirements (e.g. data type). Life history parameters (longevity, age at maturity) are relatively robust to compound bias and require only design-based protocols. Vital rate estimation demands stronger assumptions and typically requires model-based approaches with or without auxiliary data.

Step 3: Match question and data to approach. Three pathways emerge:

- *Design-based protocols* apply universally by reducing Stage 6 sampling bias ($p_{\text{sample}}(x)$) through stratified sampling and standardized necropsy. Essential foundation regardless of downstream analysis.
- *Model-based temporal analyses from carcasses* detect relative changes when (1) the question focuses on trends or comparisons, (2) sampling protocols remain consistent across strata, and (3) absolute bias quantification is unnecessary. Appropriate when $\prod p_i(x)$ can be assumed stable.
- *Model-based inference with auxiliary data* provide highest confidence when (1) absolute vital rates are required, (2) validation is needed, or (3) auxiliary data exist. Enable direct quantification of $\prod p_i(x)$ and formal bias correction.

Step 4: Adapt when constraints bind. When classical assumptions fail or sample sizes are marginal, narrow the inferential target. Observed longevity may be estimated when full survivorship curves may not. Comparative analyses across sexes or regions may succeed when absolute rates remain biased. Temporal trend detection circumvents stationarity violations that would invalidate cross-sectional life tables.

Figure 2 synthesizes this decision pathway visually, illustrating how data types (age, reproduction, covariates) flow through analytical approaches (design-based, model-based, integrated) to demographic parameters (l_x, ϕ_x, m_x, λ). This pathway embodies a fundamental principle: extract maximum information from available data while respecting inherent constraints. Rather than abandoning inference when ideal conditions are absent, adapt methods to answer narrower but still meaningful questions.

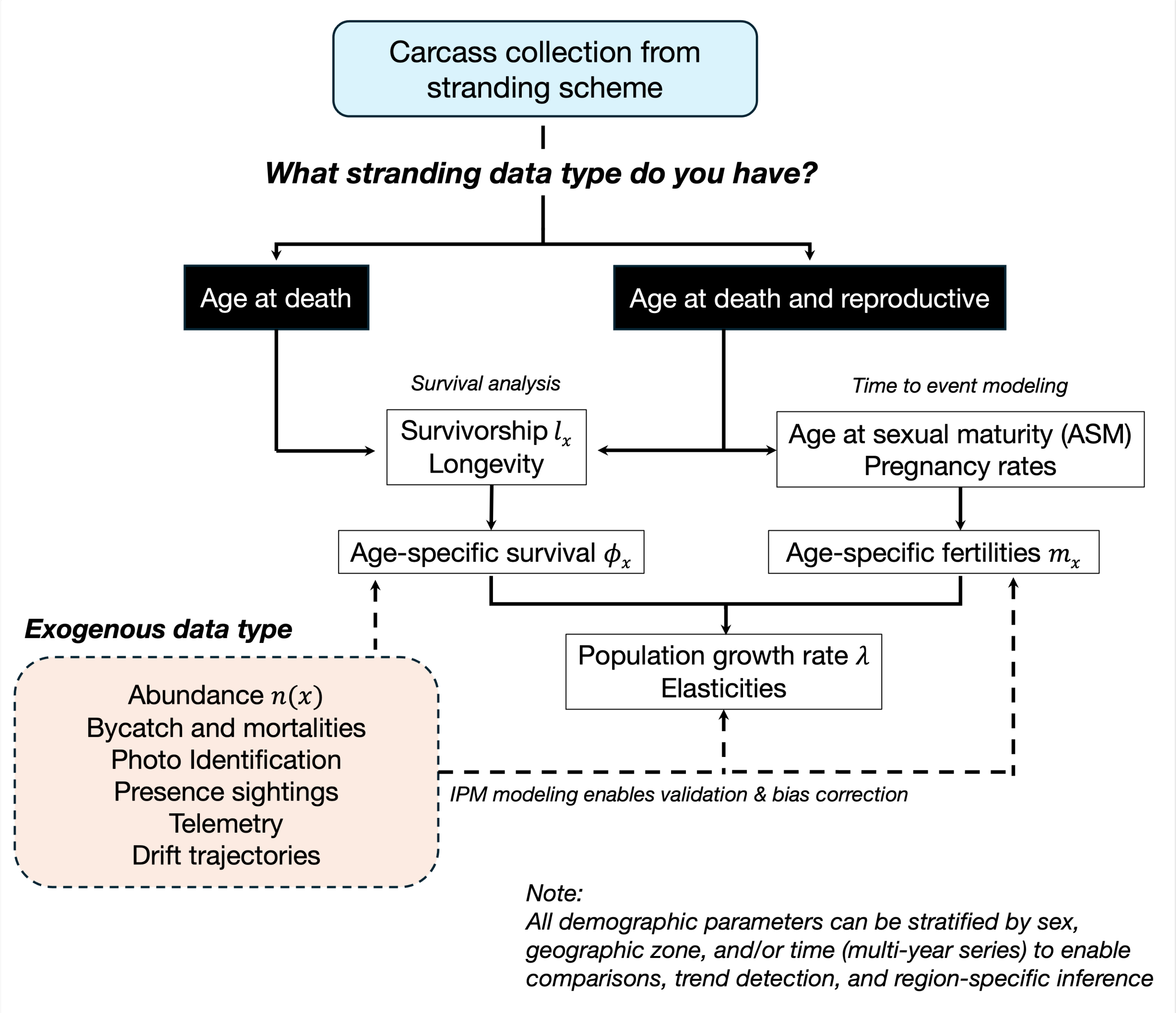

Figure 2: **Decision pathway for demographic inference from stranding data.** Age-at-death data enable survivorship curves (l_x) and age-specific survival (ϕ_x) through survival analysis. Adding reproductive status enables age-specific fertility (m_x) through time-to-event analysis. Complete vital rates permit estimation of population growth rate (λ) and elasticities via matrix population models. Exogenous data sources (abundance surveys, mark-recapture, bycatch observations, drift models) enable integrated population modeling for validation and bias correction. All demographic parameters can be stratified by sex, geographic zone, cause of death, or time to enable comparisons and trend detection.

5 The Future of Demographic Inference from Strandings

The set of best practices in Section 4 demonstrates that strandings provide reliable demographic inference: temporal trend detection, comparative analyses, and integrated modeling yield robust signals of population change. These approaches succeed by focusing on relative changes and leveraging auxiliary data to estimate reliable values and patterns of vital rates. The next frontier is to directly quantify the bias terms in Equations 1–2, transforming strandings from a valuable monitoring tool into an even more powerful demographic surveillance system.

Three research priorities will expand current capabilities: (1) systematic estimation of age/stage-specific detection probabilities enables direct conversion of observed strandings into absolute mortality probabilities by quantifying $\prod p_i(x)$ empirically; (2) incorporating spatial structure through genetics and isotopes partitions observed mortality by demographic unit, revealing fine-scale population dynamics currently aggregated; (3) bias-corrected vital rates parameterize age-structured simulation models for proactive management evaluation, moving beyond reactive abundance-based control rules. Together, these advances represent the evolution from detecting demographic change to predicting population responses under alternative management scenarios.

5.1 Quantifying Stage/Age-Specific Detection Probabilities

The central statistical challenge (confounding between true age-specific mortality probability q_x and compound detection $\prod p_i(x)$; seeEquations 1–2) can only be resolved by independently estimating each bias term. We must treat each probability component as an estimable parameter rather than an acknowledged but unquantified bias (Hart et al., 2006; Authier et al., 2014). This requires coordinated investment in drift modeling infrastructure, dedicated detection studies, and systematic data collection.

Drift modeling. GPS-tracked carcass experiments and validated transport models must systematically quantify $p_{\text{drift}}(x)$ across species, age classes, and oceanographic regimes (Peltier et al., 2012; Tavares et al., 2023; Deslias et al., 2024). Current regional applications (Peltier et al., 2013) must expand to correct observed stranding distributions for physical processes before demographic analysis. Controlled releases with satellite tracking provide empirical drift trajectories that constrain model predictions (Tavares et al., 2023).

Age-specific buoyancy and decomposition. Controlled experiments measuring carcass persistence times by size class, body condition, and season would parameterize $p_{\text{strand}}(x)$ (Moore et al., 2020). These empirical correction factors are currently absent from all demographic frameworks. Decomposition rates, gas production, and refloating potential vary dramatically with carcass size and environmental conditions (Moore et al., 2020), yet to date no studies provide age-structured estimates.

Systematic coastal observer programs. Standardized beach surveys with known effort must quantify $p_{\text{detect}}(x)$, analogous to seabird carcass surveys (Huggins et al., 2015). Comparing detected strandings against survey intensity directly estimates detection probability by carcass size and condition (Hart et al., 2006). Survey design (including observer training, transect protocols, and temporal coverage)determines whether stranding data can support demographic inference (Authier et al., 2014).

Bycatch observer programs. These programs provide the gold standard for estimating $p_{\text{cause}}(x)$ (Peltier et al., 2016, 2021; Moore et al., 2021). Comparing total fishery mortality against stranded bycatch carcasses reveals which mortality sources enter the stranding pathway. Observer coverage must be designed to ensure representative sampling across fleet segments and seasons (Authier et al., 2021).

5.2 Incorporating Spatial Population Structure and Movement

Marine mammal demography faces a fundamental challenge: classicaly it is assumed closed populations, yet marine mammals routinely violate this through complex spatial structure, seasonal migrations, and metapopulation dynamics. Classical cross-sectional methods assume all observed deaths come from a single, demographically independent population. However, stranding locations reflect the convolution of population distribution, habitat-specific mortalities, and oceanographic transport.

Bias from movement. Ignoring immigration and emigration biases vital rate estimates. Observed age distributions represent a mixture of residents and transients with potentially different demographic trajectories. CMR studies explicitly estimate immigration through recapture probabilities across space (Tenan et al., 2023), but stranding-based frameworks lack this capacity. Without quantifying movement, demographic inference conflates local dynamics with spatial redistribution: a critical blind spot.

Genetic assignment tests. These tools offer a direct solution. Multilocus genotyping of stranded individuals using microsatellites or SNPs enables probabilistic assignment to source populations (Paetkau et al., 1997; Rannala and Mountain, 1997). The method identifies immigrants whose genotypes differ from local residents. Recent applications in marine mammals demonstrate that SNP panels can detect fine-scale population structure and improve assignment accuracy (Foote et al., 2016; Parsons et al., 2024). Population genomic surveys must define demographic independence to enable this approach (Fietz et al., 2016; McCarthy et al., 2025).

Stable isotope analysis. Tissue preserve complementary information on geographic origin and movement history. Isotopic signatures reflect foraging location and distinguish residents from dispersers (Newsome et al., 2010; Hobson, 1999; Matthews and Ferguson, 2016). Combining genetic population structure with isotopic provenance enables partitioning of stranding records by demographic unit (Brotons et al., 2019; IJsseldijk et al., 2020b). This reveals whether observed mortality represents local population decline or dispersal mortality from distant sources.

Spatially explicit demographic models. Integration transforms spatially aggregated stranding data into population-specific vital rate estimates. Models must combine genetic structure (Liggins et al., 2013; Riginos et al., 2016; François et al., 2010), oceanographic drift probabilities (Cowen et al., 2006; Paris et al., 2013; Treml et al., 2015), and regional abundance (Jacobson et al., 2020; Nelson et al., 2024). Current aggregated approaches cannot separate these factors (IJsseldijk et al., 2020a; Rouby et al., 2025). This requires coordinated sampling: systematic genetic and isotopic analysis (Newsome et al., 2010; Troina et al., 2021) of strandings across regions, coupled with population genomic surveys. Spatial genetics can eliminate this blind spot (Alvarado-Serrano and Knowles, 2016; Selkoe et al., 2016).

5.3 Advancing Beyond Abundance-Based Control Rules: Demographic Management Strategy Evaluation

Traditional marine mammal conservation relies on control rules applied to abundance estimates—Potential Biological Removal (PBR), the Removals Limit Algorithm (RLA), and the Anthropogenic Removals Threshold (ART), to set allowable anthropogenic mortality thresholds (Wade, 1998; Genu et al., 2021; Ouzoulias et al., 2024). However, PBR is not a population model but a decision rule. It combines abundance, productivity, and recovery factors into a mortality limit designed to maintain populations at optimum sustainable levels, yet operates independently of the demographic processes generating population responses (Taylor et al., 2000; Lonergan, 2011).

Demographic operating models. Stranding-based vital rate estimates enable the transition to Management Strategy Evaluation (MSE) frameworks (Punt et al., 2016; Cooke, 1994; Butterworth, 2007). MSE explicitly models population dynamics through operating models parameterized by stranding-derived survivorship curves, fecundity schedules, and age structure (Moore and Read, 2008b; Saavedra, 2018; Stolen and Barlow, 2003). These frameworks simulate population trajectories under alternative control rules (PBR with varying recovery factors, RLA, or ART) and test their performance against conservation objectives over policy-relevant timescales of 50-100 years (Genu et al., 2021; Ouzoulias et al., 2024; Punt et al., 2020; Taylor et al., 2000). MSE accommodates both parametric uncertainty in vital rates and structural uncertainty in population models.

Age-structured implementation. Age-structured models become essential when age-specific mortality varies (Mannocci et al., 2012). Sensitivity analyses must identify which vital rate uncertainties most affect management outcomes (Punt et al., 2018; Brandon et al., 2017). Stranding data offer a unique advantage: they enable estimation of anthropogenic versus natural mortality components, which proves critical for evaluating whether proposed bycatch reductions achieve specified recovery probabilities (Moore and Read, 2008b; Saavedra, 2018).

Available tools. Integrated software now exists to implement MSE for data-limited species. The RLA package (Genu et al., 2021) transform stranding-derived vital rates from descriptive statistics into forward-looking conservation strategies. These tools test management actions before implementation, completing the paradigm shift from retrospective trend detection to simulation-based decision support (Punt et al., 2016, 2020).

Conclusion

Collecting stranding-based demographic data is the first step of demographic inference. Minimizing sampling bias through stratified protocols and standardized networks is essential for reliable parameter estimation. Based on the research question and data availability, practitioners should select the appropriate analytical framework: design-based for life history parameters, model-based temporal analyses with relative comparisons, or integrated population models when auxiliary data exist. Once obtained, vital rates inform conservation policies directly.

Three research priorities will expand current capabilities. Systematic quantification of age/stage-specific detection probabilities through drift modeling, controlled decomposition experiments, and coastal observer programs transforms compound bias $\prod p_i(x)$ into measurable parameters. Genetic assignment and stable isotope analysis partition stranded individuals by demographic unit, revealing spatial population structure currently obscured by aggregated analyses. Bias-corrected vital rates parameterize age-structured simulation models for management strategy evaluation, enabling proactive conservation planning rather than reactive responses to abundance declines.

The conservation stakes are high. Baiji, Caribbean monk seals, Yangtze porpoises and Vaquitas declined to extinction while abundance monitoring failed to detect deterioration in time for intervention. North Atlantic right whales provided clear demographic warnings years before abundance surveys showed decline, yet insufficient response continues. For beaked whales, offshore dolphins, porpoises, and other populations inaccessible to photo-identification or artificial marking, strandings provide the only demographic window available. Critically, this window tracks adult survival, the vital rate with highest elasticity in long-lived species. Adult survival dominates population dynamics in long-lived marine mammals, and stranding-based vital rate monitoring detects declines years before abundance impacts become statistically detectable. The best practices synthesized here: the six-stage filtering, decision tools, and analytical approaches enable extraction of meaningful demographic signals from inherently biased samples. When analyzed appropriately, demographic data obtained from stranding networks represent irreplaceable early warning systems that can prevent the next extinction rather than document it.

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