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ARTICLE

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Demographics and viability of an estuarine community of Indo-Pacific bottlenose dolphins

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Abstract

Wildlife management requires reliable demographic information to assess the status of a population and its vulnerability to threats. This study calculated age class- and sex-specific demographic parameters and assessed the viability of a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia. Boat-based photo-identification surveys ($n = 483$) were conducted between 2016 and 2019. A population viability analysis (PVA) was used to assess the community status and evaluate the effects of adult female and calf mortality, and reproduction on population growth rate. The community comprised 88 ($SD = 4.43$) individuals with a sex ratio close to parity in all but the adult age class where it was skewed towards females. Demographic changes in this community are driven by births, deaths, and the likely permanent emigration of juvenile males. No immigration was observed. The population is stable ($r = -0.004$, $SD = 0.062$) given the current demographic rates. To maintain a community of ~90 individuals, management should consider action to lower adult female and calf mortality. This should involve aiming for zero human caused mortality and ensuring adverse impacts to the population are considered in future development planning.

KEYWORDS
operational sex ratio, population viability analysis, reproductive success

1 | INTRODUCTION

Effective wildlife management requires reliable population demographic parameter estimates to assess population status, predict trends and to evaluate population's vulnerability to threats (Coulson et al., 2001; Taylor, 1995; Thomas & Kunin, 1999). However, managers often face several practical and methodological challenges in acquiring such information. First, demographic parameter estimates, as well as their accuracy and precision, vary depending on the temporal and spatial scale at which a population is observed (Thomas & Kunin, 1999). This makes meaningful demographic parameter estimates challenging to obtain for taxa, like delphinids, that are wide-ranging, long-lived, slowly reproducing, and often distributed across space without clear population boundaries. Second, although abundance, apparent survival (i.e., no distinction between death and permanent emigration), and temporary emigration rate estimates are available for several delphinid species (e.g., Nicholson et al., 2012; Slooten & Davies, 2012; Tyne et al., 2014; Zanardo et al., 2016), it is not always clear how the population in focus for management is (or should be) defined, and therefore how the demographic parameter estimates should be interpreted. Lastly, even though there is often low statistical power to detect population declines in a timeframe that allows for management interventions to halt or reverse a decline (Symons et al., 2018; Taylor & Gerrodette, 1993; Taylor et al., 2007; Tyne et al., 2016), managers commonly rely on population declines as a criterion to trigger management action (e.g., Lee Long & O'Reilly, 2009).

Given these challenges, it may often be more appropriate for managers to base decision-making on population viability analysis (PVA) that allows for the estimation of population growth rate and extinction probability based on population demographic parameters (Lacy, 1993, 2000; Thompson et al., 2000). The demographic parameters used as model inputs must be reliable if the population trajectory is to be modeled properly, and they must be interpreted based on a suitable definition of the population in question. The effects of different threats to population growth rate can be modeled by changing the input parameter values (Lacy et al., 2021; Manlik et al., 2016). These so-called sensitivity analyses can guide management action and allow managers to apply a precautionary approach depending on the projected trend for a population under different scenarios (Manlik et al., 2016; Thompson et al., 2000).

Population demographic parameters (e.g., reproductive, mortality, emigration, and immigration rates), which are required to estimate population growth rate, vary by age (Arso Civil et al., 2019) and sex (Sprogis et al., 2016; Stolen & Barlow, 2003), both of which are challenging to determine for all individuals in delphinid populations. This leads to difficulty in determining population age structure, which influences population growth rate, and in accounting for age- and sex-specific patterns in mortality and dispersal when forecasting population trends (e.g., Araújo et al., 2014; Blázquez et al., 2020; Manlik et al., 2016). Although approximate birth dates (Galezo et al., 2020; Gerber et al., 2019), individual sighting histories (Wells, 2014), and growth layers in teeth (Hohn et al., 1989) can be used to infer individuals' age, visual inspection of body length is commonly used to assign individuals into broad age classes (Parra et al., 2006; Smolker et al., 1992). This approach, however, may easily result in an incorrect assignment of age class for juvenile and adult individuals and/or lead to analytical approaches that estimate demographic parameters for adults only (Zanardo et al., 2016) or for all independent (i.e., noncalf) individuals combined (Nicholson et al., 2012; Passadore et al., 2017; Smith et al., 2013). Fortunately, recent methodological advances using noninvasive stereo-laser photogrammetry to infer the length of individuals allows more detailed population age structure to be estimated and individuals to be assigned to age classes more reliably (Cheney et al., 2018; van Aswegen et al., 2019). This enables demographic parameters to be estimated separately for different ages or age classes. Designating individuals as either male or female relies on visual observation of their genitalia, the presence of a dependent calf (Mann et al., 2000; Smolker et al., 1992) or confirmation from molecular analysis (Krützen, Sherwin, et al., 2004; Möller & Beheregaray, 2004). For some species/populations, dorsal fin markings have also been used to infer individuals' sex (Brown et al., 2016; Rowe & Dawson, 2009). Regardless of the method(s) used, the ability to investigate age- and sex-specific patterns in demographic parameters allows more refined input parameters to be used in forecasting population trends over time.

The Peel-Harvey Estuary in Western Australia is occupied by a year-round resident Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) community, which is socially, spatially, and isotopically distinct from identified communities in adjacent coastal waters (Nicholson et al., 2021b). In this study, the estuarine dolphin community is defined as the population for which demographic parameters are calculated. The population trajectory (i.e., stable, declining, or decreasing) was assessed using a PVA incorporating population age structure and age class- and sex-specific mortality rates. Additional PVA models were run to inform management options to ensure maintenance of the community. We hypothesize that the estuarine dolphin community is a relatively closed population where changes in abundance are largely determined by births and deaths.

2 | METHODS

2.1 | Study area

The Peel-Harvey Estuary ($\sim$130 km^2) is the largest estuary in southwestern Australia and is part of the Ramsar-listed Peel-Yalgorup wetland system. It is a shallow (mainly <2 m deep) microtidal (tidal range $\sim$0.5 m) estuary connected to the Indian Ocean via two openings: Mandurah and Dawesville Channels (Figure 1). Three rivers, the Murray, Serpentine, and Harvey, flow into two basins, the Peel Inlet and Harvey Estuary, from a catchment of approximately 9,400 km^2 (Valesini et al., 2019). The estuary supports migratory and other waterbirds (Hale & Butcher, 2007) and functions as an important nursery, breeding and feeding ground for numerous fish species (Hallett et al., 2019; Loneragan et al., 1986, 1987; Potter et al., 2016). The City of Mandurah, with a population of $\sim$85,000 people (Australian Bureau of Statistics, 2020), is located on the estuary with the foreshore along Mandurah and Dawesville Channels extensively modified by development (e.g., canals, breakwalls, jetties). The waterways are used for recreational activities and are important for both recreational and commercial finfish and blue swimmer crab (*Portunus armatus*) fisheries (Gaughan et al., 2019; Obregón et al., 2020).

2.2 | Data collection and photo-identification

Boat-based photo-identification surveys for dolphins were conducted between 2016 and 2019 throughout the estuary. A minimum of three predetermined transects (Figure 1) during each Austral season (Summer: December–February, Autumn: March–May, Winter: June–August, Spring: September–November) were run between January 2016 and November 2018 on board a 5.5 m vessel. Transects were completed within a day and followed the same route apart from in the Peel-Inlet where a unique zigzag pattern was followed on each sampling occasion (see example in Figure 1). The Serpentine and Murray Rivers were not part of the study design but were visited at least once every season to $\sim$7.5 km upstream. The Harvey River was inaccessible due to shallowness of the southern parts of the estuary.

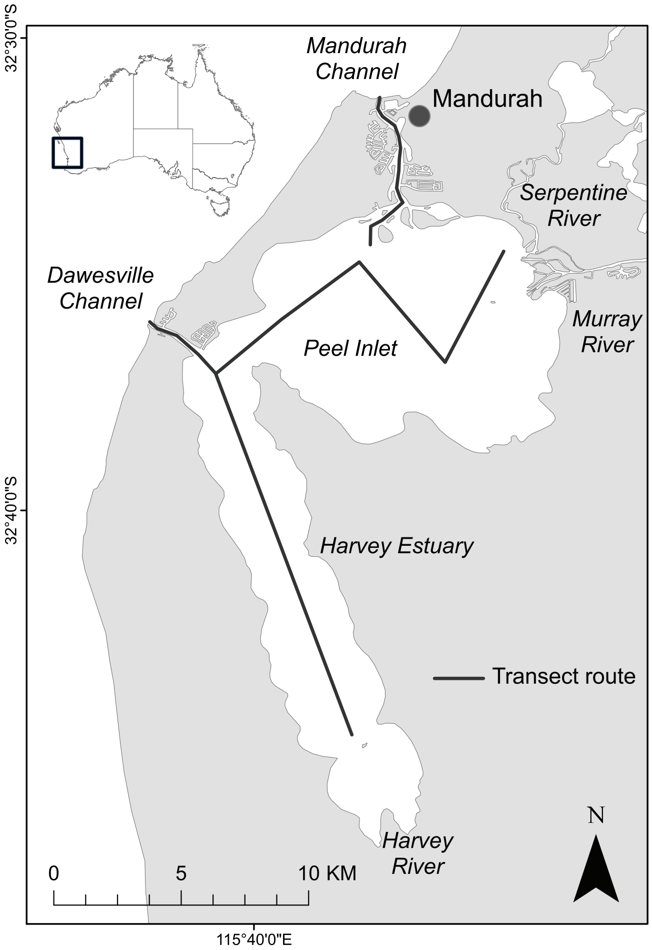

FIGURE 1 The Peel-Harvey Estuary, Western Australia, study area with an example of a transect route for boat-based photo-identification surveys targeting Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

When dolphins were encountered, a minimum 5 min survey was conducted to record the location, behavior, and group composition of sighted individuals. The dorsal fin of each individual was photographed for unique nicks and notches allowing for individual identification (Würsig & Würsig, 1977). Dorsal fin shape and additional markings, such as scarring and lesions, were used to aid in identification of individuals that had not acquired sufficient markings visible from both sides of the dorsal fin. Photographs were checked prior to leaving a group to ensure a good quality photograph (i.e., dorsal fin fully visible, in focus and perpendicular to the camera: Nicholson et al., 2012; Rosel et al., 2011; Urian et al., 1999) was obtained of each individual. Occasionally, a survey was terminated prior to obtaining good quality photographs due to the behavior of dolphins or when it was uncertain how many individuals were present in a group. The same survey protocol was applied during additional effort conducted within the estuary between 2016 and 2019 to collect tissue samples for genetic analyses and stereo-laser photogrammetry data for aging individuals (van Aswegen et al., 2019).

The best quality photograph of individuals' dorsal fin obtained during each encounter was graded for quality as per Nicholson et al. (2012). Dorsal fin photographs were compared to others in the catalog established for individuals encountered in the estuary and adjacent coastal waters. A match was confirmed by two independent observers. If there was no match, four independent observers searched the catalog for a match prior to the individual being assigned a unique identification code and added to the catalog. Only individuals identified from excellent quality photographs (as per Nicholson et al., 2012) were added to the catalog.

Supplemental information on births and deaths in the identified estuarine dolphin community (Nicholson et al., 2021b), as well as photographic confirmation of resident individuals being alive and present in the estuary, came from regular monitoring effort by the Mandurah Dolphin Volunteer Rescue Group and a tour operator, Mandurah Cruises. The resulting census-level data enabled demographic rates to be calculated directly for each age class and sex.

2.3 | Age and sex determination

For some individuals, minimum age was inferred based on a consistent association with a reproductive female and/or dependent calf or, when known, the approximate birth date. Dolphin live stranding records since 1990 (Groom & Coughran, 2012) were also used to estimate the minimum age of some individuals. Individuals >10 years of age were considered sexually mature (i.e., adults) based on information on wild (Wallen et al., 2017) and captive (Brook et al., 2000; Wells et al., 1987) dolphins elsewhere. Juveniles were identified as sexually immature based on visual inspection of their length and/or being estimated to be <10 years of age by laser-photogrammetry methods. Yearlings were defined as presumed offspring (>1 year old) of an adult female they were in infant position and consistently associated with. Offspring which were <1 year old were referred to as calves.

Approximate age of individuals was inferred from an available growth curve for the population developed as part of a separate study using data collected in the Peel-Harvey Estuary and Bunbury (~90 km south of the study area) where the age of many individuals is known (van Aswegen et al., 2019). The growth curve was developed using remote stereo-laser photogrammetry (i.e., two lasers fixed to a camera reflecting two points at a known distance (10 cm) apart on the dolphin's body when taking a photograph). The distance between a dolphin's blowhole and dorsal fin insertion is a valuable proxy measurement for total body length and can be used to infer approximate age of individuals when validated against the length of known-aged individuals (Cheney et al., 2018; van Aswegen et al., 2019). The age of immature individuals at any given length derived from the growth curve is approximate due to the variability in size of similarly aged individuals (van Aswegen et al., 2019). Age estimates may be biased for sexually mature individuals as at physical maturity (12–15 years) growth ceases due to the fusion of vertebral epiphyses (Cockcroft & Ross, 1990). Visual confirmation from photographs of genitalia and consistent association with a calf were used to identify individuals as male or female.

2.4 | Population viability analysis and demographic parameters

Population viability analyses (PVAs) were conducted using VORTEX software version 10.2.9 (Lacy & Pollak, 2017). VORTEX models wildlife population dynamics via age-based Monte Carlo simulations of deterministic and stochastic effects and estimates the population growth rate (r) and extinction probabilities under different scenarios (Lacy, 1993). It treats population processes (e.g., breeding and death) as discrete, sequential events, with probabilistic outcomes and calculates a mean population growth rate based on a cohort life-table with mean birth and age specific mortality rates that are determined by the user. Population demographic parameters (e.g., population size, age, and sex structure, annual mean reproductive and mortality rates), required as input parameters for the model, were calculated for the dolphin community using data collected between 2016 and 2019 (see Table 1). The VORTEX models were run with 1,000 iterations for 100 timesteps (i.e., years) with extinction defined as only one sex remaining in the population.

The initial population size for the models was determined by the number of individuals alive in the defined estuarine social community in 2016 (Nicholson et al., 2021b). Known (i.e., from birth records), estimated (i.e., from

TABLE 1 Demographic parameters used for a Population Viability Analysis for a resident community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) occupying the Peel-Harvey Estuary in Western Australia.

Model parameter	Input value
Initial population size (individuals)	86
Carrying capacity (individuals)	150
Age class distribution (%)	
Calves	F = 8.14 M = 3.49
Yearlings	F = 5.81 M = 11.63
Juveniles	F = 11.63 M = 15.12
Adults	F = 29.07 M = 15.12
Reproductive system	
Age of female maturity (years)	10
Age of male maturity (years)	10
Maximum age (years)	40
Sex ratio at birth	50:50
Reproductive rate (%)	38.54 (SD_{EV} = 14.37)
Males in breeding pool (%)	56.5
Weaning age (years)	3
Mean annual mortality rates (%)	
Calves (males and females combined)	24.76 (SD_{EV} = 1.51)
Yearlings (males and females combined)	0 .00 (SD_{EV} = 1.51)
Juvenile males	12.70 (SD_{EV} = 1.51)
Juvenile females	8.87 (SD_{EV} = 1.51)
Adult males	6.28 (SD_{EV} = 1.51)
Adult females	5.05 (SD_{EV} = 1.51)

Note. Parameter estimates reflect population structure in 2016. F = female, M = male, SD_{EV} = standard deviation due to environmental variance.

stereo-laser photogrammetry measurements) and best guess (i.e., from calving or live stranding records) ages were used to create a population age distribution for both sexes in 2016. This was used as the initial age distribution for a base model (Figure S1). Immature individuals, based on visual inspection of their length, whose age was not known or estimated, were assigned to be 6 years old (i.e., the age at midpoint in the juvenile age class). Unknown age adults were assigned to be 23 years old (i.e., the age at midpoint in the adult age class). The maximum age of reproduction was set to 35 years for both sexes based on the oldest individual, a female, observed in the system living to at least 33 years old (assuming she was at least 10 years old when she had her first calf) while producing a calf at 32 years old and the oldest male estimated to have died at 35 years old, based on being at least 6 years old at first live stranding.

The carrying capacity for dolphins in the Peel-Harvey Estuary is unknown and may vary among years and seasons in response to primary production or prey availability (Young & Phillips, 2002). To allow for population expansion, the carrying capacity for the base model was set to 150 individuals.

An annual reproductive rate was calculated by dividing the number of calves born by the number of sexually mature females in the estuarine community within a given calendar year. The mean annual reproductive rate was used as an input parameter for the base model. As death and permanent emigration could not be fully separated, annual mortality rates were calculated as the proportion of individuals that were confirmed deceased or disappeared (i.e., not observed over two sampling seasons) from the community during a calendar year. Mean annual mortality rates were calculated separately for each age and sex class and were used as input parameters for the PVA: calf mortality rate was applied to ages from 0 to 1, yearling mortality rate from one to three, juvenile mortality rate from three to ten, and adult mortality rate from age ten onwards. Standard deviations due to environmental variance (SD_{EV}), which refers to variation in demographic parameters due to random fluctuations in the environment (e.g., weather, prey availability, predation pressure), were calculated for reproductive and mortality rates. Environmental variation was modeled by drawing random numbers from binomial distributions in which the percentage of females reproducing and individuals dying each year were drawn from normal distributions with user-specified mean and SD_{EV} (Lacy 1993; Lacy et al., 2017). Given the short duration of this study and low interannual variability in non-calf mortality rates, it was not possible to separate SD_{EV} for adult, juvenile, and yearling mortality rates. As such, the SD_{EV} for calf mortality rate was applied to all mortality rates. Alternative SD_{EV} values were trialed by decreasing and increasing SD_{EV} by 0.5 increments up to the value of total observed variation while keeping all other input parameters the same. Given the similarity in estimated population growth rates and extinction probabilities (Table S1), the alternate SD_{EV} values are not considered or discussed further. Environmental variation in reproduction and mortality were modelled independently from each other.

There is no population specific information on genetic structure, including inbreeding, or the proportion of males that contribute to the gene pool; both parameters can be incorporated in the PVA. Given members of the estuarine community interact with members of coastal communities (Nicholson et al., 2021b), which likely facilitates gene flow between communities, inbreeding depression was not considered in the model. Following Manlik et al. (2016) the proportion of males contributing to the gene pool was set to 56.6%, which is a midpoint of possible values between 13% and 100% reported by Krützen, Barré, et al. (2004) for bottlenose dolphins in Shark Bay, Western Australia.

To explore the effect of carrying capacity (K) on the estimated population growth rate, two additional models were run: one with $K = 86$ individuals (i.e., system is at carrying capacity) and one with $K = 100$ (i.e., to allow for slight population expansion). Additionally, a model with stable population age structure (estimated from a life table in VORTEX), as opposed to the observed age structure specified in this study, was run to investigate whether this had an impact on the resulting population growth rate. To inform management, 12 further models were run to evaluate the effect, or combined effect, of (1) increased reproduction, (2) decreased adult female, and/or (3) calf mortality on population growth rate. Keeping all other parameters as described above (i.e., the base model), mean annual reproductive rate was increased and adult female and calf mortality rates were decreased by 1%, 5%, and 10%.

Although not required as input parameters for the model, apparent survival and immigration rates were also calculated. Individuals were confirmed deceased only if they were observed postmortem. Individuals that were not observed in two consecutive sampling seasons (i.e., 6 months) were considered as having either died or emigrated. Calves were assumed deceased if their mothers were observed without them on more than three occasions. The apparent annual survival was calculated for each age class (i.e., adults, juveniles, yearlings, and calves) as the proportion of individuals alive in the community during a calendar year surviving to the subsequent calendar year. Immigration rate was calculated as the proportion of individuals that were observed to consistently associate with members of the defined estuarine community for at least two consecutive seasons (i.e., 6 months).

3 | RESULTS

3.1 | Effort and group encounters

Thirty-seven transects were conducted in the Peel-Harvey Estuary between January 2016 and November 2017 equating to approximately 350 hr of effort. Additionally, during this time, opportunistic search effort throughout the estuary was conducted on 48 days (~253 hr). A total of 628 dolphin groups were encountered, of which 483 comprised estuarine resident dolphins (Nicholson et al., 2021b). The remaining groups were encountered in Dawesville

Channel and comprised solely of individuals identified as part of social communities residing in coastal waters (Nicholson et al., 2021b). Thirteen transects were conducted in the estuary in 2018 (~109 hr) with additional effort conducted on six days (~40 hr). This effort resulted in 177 dolphin group surveys. In 2019, six days (~43 hr) were spent in the estuary with a further 50 dolphin groups encountered.

3.2 | Community age and sex structure

The dolphin community comprised on average 11% calves, 15% yearlings, 32% juveniles, and 42% adults (see estimated ages of all individuals in Tables S2–S4). Sex ratios were approximately equal in all age classes, except adults, where 33% were males and 67% females (Table 2).

3.3 | Demographic parameters and population viability analysis (PVA)

Between January 2016 and December 2019, an accumulative number of 113 individuals were identified as part of the estuarine dolphin community with a mean of 88 ($SD = 4.43$, range = 84–94) individuals alive at the end of each calendar year. The initial population size in 2016 was 86 individuals. A total of 37 calves were born to 25 estuarine resident females during this study (Table S2). An annual variability from 5 to 16 ($M = 9.25$, $SD = 4.99$) was observed in the number of calves being born. This related to the number of females available to produce a new calf, i.e., females whose calf was 2 or 3 years old, females who had lost a calf, or females who had become mature. Births were observed between November and June with the majority (73%) of calves born between March and May (Figure S2). Three individuals, estimated between 8 and 15 years of age (at the time of giving birth), had their first calf during this study. An additional female was confirmed mature from a postmortem examination (i.e., ovarian scarring consistent with one ovulation event) but had not produced a calf. The mean annual reproductive rate for the community was 0.39 ($SD = 0.20$). The observed interbirth interval was between 2 and 4 years ($M = 3.30$, $SD = 0.86$) when considering females that successfully weaned their previous calf.

Eighteen individuals were confirmed deceased and a further 11 either died or emigrated from the estuary (Table 2). Juvenile males contributed 54.5% ($n = 6$) to individuals that either died or emigrated while other age/sex classes contributed <18.2% each. Juvenile males and females both contributed 11.1% to confirmed mortalities, while adult females contributed 22.2%, adult males 5.6%, and calves 50.0%. Overall, apparent survival rates varied among

TABLE 2 Population demographic parameters for a community of 88 (*SD* = 4.43) Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary. Parameters were calculated from photo-identification data collected year-round between 2016 and 2019. All values apart from number of individuals deceased or emigrated are presented as a mean (*SD*) over the study period. Age class and sex of all individuals identified as part of the estuarine social community were known. Individuals were confirmed deceased only if observed postmortem, while those considered deceased or having emigrated from the community were not observed during a period of at least 6 months.

Age class	Community composition Mean % (*SD*)	Sex ratio (M:F)	Apparent survival Mean (*SD*)	Deceased individuals (*n*)	Deceased or emigrated individuals (*n*)
Adults	41.80 (3.01)	33:67	0.95 (0.02)	5	3
Juveniles	32.40 (6.00)	58:42	0.88 (0.03)	4	8
Yearlings	15.41 (6.98)	47:53	1.00 (0.00)	—	—
Calves	10.39 (5.06)	50:50	0.75 (0.19)	9	—

age classes with the lowest survival observed for calves and the highest for yearlings. There was no immigration to the estuarine dolphin community during this study nor was any individual not part of the defined social community observed consistently in the estuary.

The base PVA model using input parameters summarized in Table 1, forecast a population with a slightly negative mean population growth rate ($r = -0.004$, $SD = 0.062$; Figure 2). The estimated extinction probability was 0.010 ($SE = 0.003$) with estimated 67 ($SD = 35$) individuals alive in 100 years.

The model with stable age distribution estimated near identical population growth rate and extinction probability as the base model (Table 3). Assuming the population is currently at carrying capacity or allowing for only a slight expansion of the population, however, resulted in reduced population size and increased, although still very low, extinction probabilities over 100 years (Tables 3 and S5). The PVA models with adult female mortality decreased by 10% resulted in a positive mean population growth rate (*r*) with ~90 individuals alive and zero probability of extinction in the next 100 years (Table 3). A model with a 10% increase in reproductive rate and one with a combination of

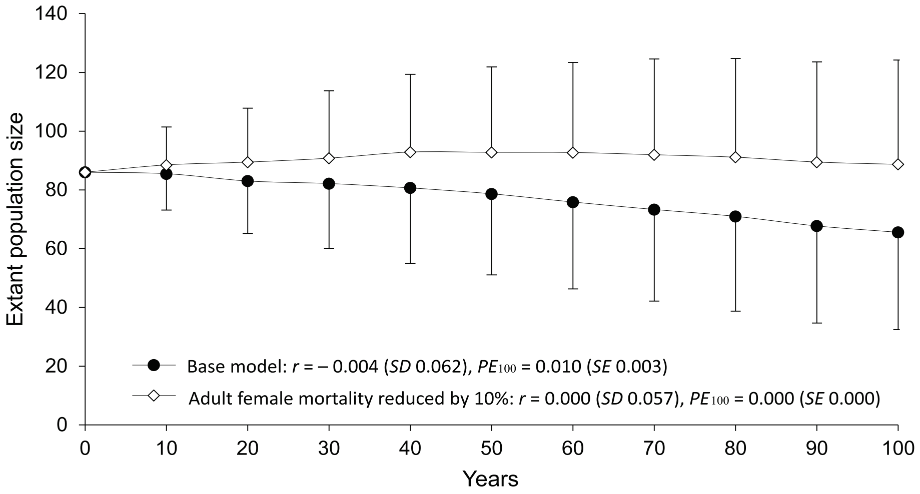

FIGURE 2 Population trajectories modeled by Monte Carlo simulations of deterministic and stochastic effects for a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: r = population growth rate, PE_{100} = probability of extinction in 100 years.

TABLE 3 Effects of parameter variation on mean population growth rate (*r*), probability of extinction (*PE*) and population size in 100 years forecast for an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population resident to the Peel-Harvey Estuary in Western Australia.

Model	K	AFm	Ym	RR	*r* (*SD*)	*PE* (*SE*)	*N* (*SD*)
PVA_base	150	5.05	24.76	38.53	−0.004 (0.062)	0.007 (0.003)	67 (35)
PVA_stable_age_distribution	150	5.05	24.76	38.53	−0.004 (0.062)	0.009 (0.003)	66 (35)
PVA_K_86	86	5.05	24.76	38.53	−0.004 (0.066)	0.010 (0.003)	49 (21)
PVA_K_100	100	5.05	24.76	38.53	−0.004 (0.063)	0.011 (0.003)	55 (24)
PVA_RR_+10%	150	5.05	24.76	41.52	0.000 (0.057)	0.002 (0.001)	90 (37)
PVA_AFm_−10%	150	4.55	24.76	38.53	0.000 (0.057)	0.000 (0.000)	89 (36)
PVA_AFm_−5%_Cm_−10%	150	4.80	22.13	38.53	0.000 (0.041)	0.001 (0.001)	90 (37)

Note. K = carrying capacity, AFm = adult female mortality rate, Cm = calf (i.e., individuals <1 year old) mortality rate, RR = reproductive rate, *SD* = standard deviation.

5% and 10% decrease in adult female and calf mortality, respectively, also produced a positive *r* but forecast a very low probability of extinction in the next 100 years.

4 | DISCUSSION

This study found that the resident Peel-Harvey Estuary community of approximately 90 dolphins comprise individuals of all ages and both sexes. Although the calf, yearling, and juvenile sex ratios were close to parity, there was nearly twice as many adult females than males in this community. The population trajectory was modeled considering community age and sex structure and age class- and sex-specific mortality rates. The mean population growth rate was slightly negative but the probability of extinction in the next 100 years was low. Additional PVA models suggested that decreasing adult female and calf mortality rates or increasing the reproductive rate would result in higher population growth rate. No immigration into the community was recorded during the study. This suggests additions to the community are solely through births.

4.1 | Reproduction and calving success

The mean annual female reproductive rate (38.54, $SD = 20.00$) in the Peel-Harvey Estuary dolphin community was higher than those that have been reported for other Indo-Pacific bottlenose dolphin populations. For example, Manlik et al. (2016) estimated an annual reproductive rate of 13.58 ($SD = 8.64$) for a population of dolphins in Bunbury, approximately 100 km south of the study area. Three-year reproductive rates of 40.74 ($SD_{\mathrm{EV}} = 13.54$) and 58.35 ($SD_{\mathrm{EV}} = 9.38$) were also estimated for dolphin populations in Bunbury and Shark Bay, Western Australia, respectively (Manlik et al., 2016). During this study, all mature females gave birth within a 3-year interval, with some females giving birth on multiple occasions (i.e., resulting in a 3-year reproductive rate of >100%). The mean annual reproductive rate was also higher than that reported for a well-studied bottlenose dolphin (*Tursiops truncatus*) population in Sarasota Bay, Florida (Lacy et al., 2021). It is possible that the higher reproductive rates observed in the Peel-Harvey Estuary, in part, reflect the high level of year-round monitoring of this community whereby most births are detected (Table S2). This suggests, generally, that reproductive rates and calf mortality rates are likely underestimated when using incomplete records or without reference to a clearly defined population.

4.2 | Apparent survival and adult sex ratio

The relatively high apparent survival rate for adults in the estuary was comparable to that estimated for a *T. aduncus* population in Bunbury and slightly higher than estimated for a population in Shark Bay, Western Australia (Manlik et al., 2016). There were, however, approximately twice as many mature females than males in the Peel-Harvey Estuary dolphin community despite sex ratios being close to parity in both dependent individuals and juveniles. Similarly, Kogi et al. (2004) found that while subadult sex ratio in a population of *T. aduncus* around Mikura Island in Japan was significantly skewed towards males, the adult sex ratio was significantly skewed towards females. In contrast, Manlik et al. (2016) reported a sex ratio slightly skewed towards females (i.e., 45:55) for a population in Bunbury and an equal sex ratio for a population in Shark Bay. In the Peel-Harvey Estuary dolphin community, higher adult male mortality could, over time, lead to the observed skewed sex ratio (e.g., Scott et al., 1990). Another possibility could be permanent emigration by juvenile males, which were the most observed age/sex class to disappear from the estuary while their confirmed mortalities were low. Similar observations were made for a common bottlenose dolphin (*T. truncatus*) population in Sarasota, Florida, where 83.3% of deceased or permanently emigrated individuals were juvenile males (Wells & Scott, 1990). It is typical for mammals with promiscuous mating systems, like dolphins (Connor et al., 1996), to have a high proportion of juvenile males to permanently emigrate in response to competition for mates and to achieve outcrossing (Dobson, 1982). This type of dispersal would produce vagrant males who would either establish a new home range excluding their natal range (Lidicker, 1975) or remain nomadic. Many studies on bottlenose dolphins report a proportion of individuals sighted to having been observed only once and labeled as transient in relation to a study area (e.g., Chabanne et al., 2017; Fury & Harrison, 2008; Möller et al., 2002; Nicholson et al., 2021b). Here we suggest that some of these individuals could be emigrant males looking for mating opportunities or to permanently occupy a socially vacant niche (Saltz et al., 2016). In this study, individuals who may have permanently emigrated from the study area have not been identified since their disappearance. This was despite them being sufficiently “marked” and substantial survey effort in coastal waters adjacent to the estuary. This suggests it is possible that not all bottlenose dolphin males continue to use part of their natal range as reported by other studies (e.g., Krützen, Sherwin, et al., 2004; Scott et al., 1990; Tsai & Mann, 2013). It could be that subordinate juvenile males adopt a strategy of permanently emigrating to ensure nonzero fitness (e.g., Saltz et al., 2016). This hypothesis requires further investigation for the Peel-Harvey Estuary dolphin community.

Although the Peel-Harvey Estuary dolphin community comprises more than twice as many adult females than males, the operational sex ratio (i.e., the ratio between potentially receptive males to receptive females at any given time; Emlen, 1976) may still be unfavorable for males in years when the number of females in estrus is low. The number of estrous females (based on births and the number of females with dependent calves each year; Table S2) varied between five and 18 during this study. As such, regardless of the skewed adult sex-ratio, males face higher competition for females during the years when there is low availability of estrous females. Increased male bias in operational sex ratio may lead to increased male aggression and mate defense (Weir et al., 2011) and is expected to lead to male alliance formation (Diaz-Aguirre et al., 2018; Whitehead & Connor, 2005). Although alliance formation in the Peel-Harvey Estuary community needs further investigation, it is possible that males that are part of the estuarine community respond to increased competition in some years by herding females outside the community. During 2016 and 2017 when there were five and six estrous females (based on calving records the following year and all other mature females being with a dependent calf) in the Peel-Harvey Estuary community, respectively, males were observed with coastal females within the estuary. These females were not observed in estuarine waters on any other occasions. Future studies on consortships would provide better understanding on male reproductive strategies in this community.

4.3 | Population viability and management priorities

The community can be considered stable over time should the demographic rates remain as described. Regardless, given that immigration was not recorded, the estimated growth rate makes the community vulnerable to external stressors that may affect individuals' survival or reproductive success.

The demographic parameters calculated and used as PVA inputs for the base model were considered largely unbiased. All individuals identified as part of the estuarine community (as per Nicholson et al., 2021b) were regularly sighted to confirm they were alive and resided in the estuary. Carcasses were retrieved/identified for a relatively high number (45%) of individuals (adults and juveniles) that went missing from the community. Additionally, all sexually mature females were observed either with a calf or a yearling throughout the study, leading to the assumption that all births, apart from possibly one, were detected. Due to known and estimated ages for most individuals, it was possible to define a population age structure and reliably assign individuals into age classes. The sex of all individuals in the community, including calves, was also known. This allowed for stage (i.e., juvenile/adult) and sex-specific apparent survival to be incorporated in modeling the population trajectory and extinction risk. It is recommended that longer term data are collected to increase confidence in capturing the true variation in population demographic parameters and to validate the model projection described in this study (Lacy et al., 2021).

To change the forecast population trajectory and to maintain a resident population of ~90 dolphins, results of the alternate PVA models suggest management action should aim to retain the estuary's carrying capacity while decreasing adult female and calf mortality and/or to increasing reproductive rates. The primary focus should be given to reducing adult female and calf mortality as the population appears to currently be at reproductive capacity. This is based on all mature females having given birth as expected every 2–4 years while having a dependent calf during the years when they did not reproduce. Reducing adult female and/or calf mortality by 10%, or even just 5% annually, however, is also not possible given the low number of individuals lost each year. As such, it is recommended that no more than an average of one adult female is lost from the community each year, while considering action to reduce calf mortalities over time. To ensure effective management action is taken, further research is required to investigate the main causes of mortality in this community and to separate natural from nonnatural (e.g., mortality linked to fishing line entanglements, vessel strikes, or contaminants) mortality.

Discarded recreational fishing gear poses a risk to the health of individuals in the Peel-Harvey Estuary dolphin community. The estuary is an important fishing area for recreational fishers, with commercial fishers also operating in the area (Gaughan, 2019; Hale & Butcher, 2007). No adverse impacts from commercial fishing have been recognized for this community; however, five individuals and an additional three coastal dolphins who regularly use the Dawesville Channel, have been observed entangled in recreational fishing gear between 2016 and 2021. Discarded fishing gear has also been identified as a major threat to marine megafauna globally (Moore et al., 2009; Stelfox et al., 2016) with recreational fishing gear, mainly fishing line, affecting estuarine and coastal bottlenose dolphins (Mann et al., 1995; Marks et al., 2020; McHugh et al., 2021; Miketa et al., 2017; Wells et al., 2008, 2013). Educating the public on impacts of discarded fishing gear on wildlife is imperative to deal with the source of the problem while building capacity in local dolphin incident response to ensure quick disentanglement of individuals (Wells et al., 2008, 2013).

A relatively high number of dolphin live strandings have been recorded in the Peel-Harvey Estuary (Groom & Coughran, 2012). Live stranding events likely contributed to 21% of mortalities recorded during this study. Most live stranded dolphins have been individuals deemed in good health (based on poststranding survival) that have gotten caught by low tides behind or on sandbars, with mortalities mostly related to individuals suffering severe sunburn. Monitoring for live strandings during summer months (i.e., when individuals are at elevated risk of getting severely sunburnt) and ensuring a quick response to relocate stranded individuals to deeper water should remain a management priority that may aid in reducing adult female mortality in this community. For marine mammal populations, depending on their population growth rate, some human caused mortality may be acceptable (Gerrodette, 1996; Parra & Cagnazzi, 2016; Read & Wade, 2000). In such cases, a potential biological removal (PBR) can be calculated. The PBR estimates the maximum number of individuals that may be removed, excluding natural mortality, while allowing a stock (i.e., a group of marine mammals of the same species in a common spatial arrangement that interbreed when mature) to reach or maintain an optimum sustainable population (U.S. Marine Mammal Protection Act 1972; Wade, 1998). Given the slightly negative mean population growth rate estimated by the base model for the Peel-Harvey Estuary dolphin community, it is not appropriate to calculate PBR for this community. Management should aim for zero human caused mortality (e.g., mortality due to fishing line entanglements), decreased mortality due to live strandings, and maintenance of the currently high reproductive rate for this community.

Exposure to other human activities (e.g., boating, dredging, noise, pollution) can also lead to direct and indirect impacts on dolphins including animals moving temporarily or permanently away from an area (Bejder et al., 2006; Pirotta et al., 2013; Watson-Capps & Mann, 2005). Additionally, there may be population level consequences through lowered reproductive success (Kemper et al., 2019; Senigaglia et al., 2019), increased mortality (Wells et al., 2008; Wells et al., 2013), and decreased health of individuals (Twiner et al., 2011; Wells et al., 2005). The Peel-Harvey Estuary has been highly modified over time with a second entrance, Dawesville Channel, engineered in 1994 to relieve symptoms of eutrophication (Brearley, 2005; Elliott et al., 2016). Additionally, multiple canal systems, break walls and other structures have been constructed, in particular along both entrance channel foreshores. These structural modifications have resulted in changes in the ecosystem (Hale & Butcher, 2007; Potter et al., 2016) that have likely influenced the carrying capacity of the Peel-Harvey Estuary for dolphins. Variations in prey availability within the estuary may also shape the way dolphins use the estuary with potential range expansions to coastal waters (Henderson et al., 2013; Wilson et al., 2004) if there is insufficient biomass of fish to meet the community's high energetic demands (Nicholson et al., 2021a). The PVA models with reduced carrying capacity for the system resulted in decreased community size over time. As such, an entire ecosystem approach to management is required to ensure the system can support >100 dolphins. The human population of City of Mandurah, which fringes the estuary, is forecast to increase (https://forecast.id.com.au/mandurah), which will likely lead to further human use of the estuary and development around it. It is recommended that future development planning considers impacts on the resident dolphin community, which relies on estuarine resources (Nicholson et al., 2021a), to ensure its persistence over time.

4.4 | Conclusions and recommendations

Based on the findings of this study, demographic changes in the resident Peel-Harvey Estuary dolphin community are driven by birth and death processes, as well as the likely emigration of immature males. Although the adult sex ratio was highly skewed toward females, the operational sex ratio in 2016 and 2017 was highly skewed toward males. With the current population structure and calculated demographic rates, the community is stable but vulnerable to adverse impacts that affect individuals' survival and reproductive success.

It is recommended that a longer-term data set is established and demographic parameter values and PVAs presented in this study are revised periodically. As a precautionary approach, management should aim for zero human caused mortality while building capacity to detect and quickly respond to dolphin incidents (i.e., entanglements and live strandings) in the estuary. Future development planning should consider impacts on dolphins, to ensure reproductive output of this community is maintained (i.e., prioritize protection of mature females). Long-term, systematic monitoring (i.e., Hawkins et al., 2017) of this population is recommended to detect changes in population age and sex structure as well as demographic parameters which may lead to a changed status of the population.

AUTHOR CONTRIBUTIONS

Martin van Aswegen: Investigation; methodology; writing – review and editing. **Neil Loneragan:** Conceptualization; supervision; writing – review and editing. **Lars Bejder:** Conceptualization; funding acquisition; resources; supervision; writing – review and editing. **Krista Nicholson:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing–original draft.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

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