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Assessing the growth rate of endangered Franciscana dolphin in Argentina, South America

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ABSTRACT

Cetacean populations are vulnerable to decline due to anthropogenic threats and life history traits. The Franciscana dolphin (*Pontoporia blainvillei*) has been considered the most affected small dolphin in the Southwestern Atlantic Ocean. In this study a method is presented for estimating the growth rate of the Franciscana dolphin affected by incidental mortality (bycatch) in coastal marine areas of Argentina, South America. We used a general approach based on vital parameters information such as reproductive rates and survival probabilities for an age-structured population. The Franciscana's growth rate was estimated using Leslie's approach through an algorithm implemented in a 14 × 14 matrix model. Then, the population was characterized analysing the discrete-time evolution of the age–population vector. We found that the potential growth rate <1 indicates that Franciscanas in Argentina are susceptible to decline under current levels of incidental mortality.

1. Introduction

Marine and coastal environments are increasingly affected by several anthropogenic impacts, which in particular disturb charismatic megafauna such as cetaceans. In the Southwestern Atlantic Ocean, the Franciscana dolphin, *P. blainvillei* is vulnerable to incidental mortality in gillnet fisheries (Secchi et al., 1997, 2003; Crespo et al., 2010; Denuncio et al., 2019). Since 1940s this anthropogenic stressor (bycatch) has been occurring alongside its geographical distribution (Di Beneditto and Ramos, 2001; Bertozzi and Zerbini, 2002; Kinas, 2002; Secchi and Fletcher, 2004; Cappozzo et al., 2007; Negri et al., 2013; Prado et al., 2013; Secchi, 2014). More than 400 dolphins have been accounted to be caught annually in gillnets on coastal waters off Argentina (Bordino and Albareda, 2004; Negri et al., 2013). Moreover, incidental annual mortality of the Franciscana dolphin in the area represents up to 2%–5% of its abundance (Crespo et al., 2010; Negri et al., 2013). According to the International Whaling Commission Scientific Committee, this rate of bycatch is likely unsustainable for any small cetacean (Barlow and Boveng, 1991). Considering that the species abundance has been projected to decline by more than 30% in a period of three generations (Secchi, 2006) it has been classified as vulnerable to extinction by the International Union for Conservation of Nature (IUCN) (Reeves et al., 2012). Almost a decade later, the Franciscana dolphin continues facing the same threats due to lack of fisheries regulations, throughout the entire region of South America. Reliable estimation of biological parameters such as population growth rates of cetaceans is needed to subsidize sounding viability analysis and conservation strategies (e.g. Wade, 1998; Secchi, 2006; Moore and Read, 2008; Alava et al., 2012, 2017). In this sense, several studies are being conducted and information derived from bycatch specimens is and particularly useful to estimate population parameters for population modelling and for addressing management and conservation issues (Secchi, 2006; Secchi et al., 2003; Cáceres and Cáceres-Saez, 2013; Prado et al., 2013; Secchi, 2014; Gariboldi et al., 2015).

The prediction of population dynamics is one of the mainstays of theoretical and applied ecology (e.g. Caswell, 2001). Population ecology uses models to evaluate the performance and to make predictions of the population viability; and specifically the assessment of growth rate is a fundamental demographic

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parameter. The models can be used to evaluate the effects of the removal of individuals from a population and are particularly useful in understanding the constraints on population growth imposed by the life history parameters (Barlow and Boveng, 1991; Caswell et al., 1998). The survival and mortality rates can be inferred by following cohorts through time; or indirectly from analysis of an age-distribution of living individuals, and an age-distribution of deaths (Caughley, 1966). Each method involves restrictive assumptions that are unlikely to be met exactly but are often approximated enough for practical purposes. It is well accepted that for terrestrial mammals life tables can be ready-made. The mortality is a crucial vital parameter that can be accepted to be almost constant across the age-classes. For example, typical mammalian life span can be age-grouped into three categories: high juvenile mortality, mature age-group with low mortality, and a third group of elderly members of increasing mortality (Caughley, 1966; Spinage, 1972) as survivorship curve describes. Although, both rates (survival and mortality rates) can be estimated, there are difficulties in applying this approach. Frequently, a population is not in a stable age-distribution, or if it is, the age-distribution cannot be determined without biased data (e.g. Caughley, 1966). Generally, one or more age classes are often missing or are unrepresentative in the sample. In this context, it is difficult to obtain samples large enough to estimate the age- or stage-specific rates accurately.

It is well known that many population analyses underscore the considerable uncertainty that exists regarding potential rate of increase (Taylor and Gerrodette, 1993; Taylor et al., 2000) thus, we are forced to accept uncertainties in vital parameters. These variations can be assumed to be a stochastic (Tuljapurkar, 1982; Tuljapurkar et al., 2003) or to have random values (Gerrodette et al., 1985; Caswell et al., 1998). The random vital parameter has shown to be an important component of calculating the growth rate in an age-structured Leslie model (Cáceres and Cáceres-Saez, 2011). Furthermore, the correlations between vital parameters should be considered in those descriptions (Cáceres and Cáceres-Saez, 2013). The sensitivity analysis in Leslie's approach has shown that the dominance is linked to survival rates, rather than fecundity (Fifas et al., 1998). The variance in vital parameters has been limited to the sensitivity analysis (Caswell, 1978), and this study shows how much the variance in Leslie's matrix elements contributes to the dispersion in the growth rate (Brault and Caswell, 1993; Caswell, 2019).

The situations in which vital parameters take into account incidental mortality contributions can be calculated by perturbation theory. In fact, in order to calculate the growth rate from the time-evolution of the population vector, the problem must be placed in correspondence with a random Leslie approach. Then, the growth rate can be calculated in terms of the asymptotic long-time behaviour of the population vector state i.e., an effective Perron–Frobenius eigenvalue λ_{eff} can be defined (Cáceres and Cáceres-Saez, 2011; Cáceres, 2017). The dominant zero of the characteristic polynomial of a random Leslie matrix is the inverse of the growth rate, and strongly depends on the distribution of matrix elements (Leslie, 1945; van Groenendael et al., 1988; Cáceres and Cáceres-Saez, 2011). Although it was acknowledged that this issue is likely to underestimate the accuracy of the growth rate, few attempts have been made to correct this value due to the lack of statistical data in the vital parameters. These mentioned calculations, considering different distributions and correlations, can also be implemented solving a random Leslie recurrence relation which leads to the calculation of an effective eigenvalue λ_{eff} (equivalent to the effective growth rate as reported by Pool and Cáceres (2010).

In the current study, our approach to the uncertainty has the same scope of the approach described by Hilborn and Mangel (1997), where models are fitted to data using likelihood functions, and biological parameters are estimated from available data. Therefore, the main objective in this work is to calculate the rate of increase of the Franciscana dolphin population under incidental mortality, but only considering the mean-values of bycatch in Argentina, South America.

2. Material and methods

2.1. The Age-Structured Leslie Model

Population growth rate λ is calculated by using the recurrence relation:

$$\mathbf{X}(m+1) = \mathbf{M} \cdot \mathbf{X}(m) \tag{1}$$

where, $\mathbf{M}$ is Leslie's matrix and $\mathbf{X}(m)$ is the age-structured population vector state at time m (Leslie, 1945), *i.e.*: $\mathbf{X}(m)_j$ is the jth component of the vector population at discrete time m, representing the concentration at the age j. The corresponding invariant population vector $\Psi > 0$ can be calculated using incidental mortality mean-values. Thus, we will solve the linear algebra problem: $\mathbf{M} \cdot \Psi = \lambda\Psi$ using the corresponding Perron–Frobenius eigenvalue $\lambda > 0$ of Leslie's matrix (Cáceres, 2017).

We consider that elements in the Leslie matrix $\mathbf{M}$ (of dimension NxN) may have contributions with parameters varying around their mean-values by man-made interferences. For this assessment we use vital parameters of Franciscana dolphins from Argentina (Panebianco et al., 2012; Negri et al., 2013) and schedules of natural mortality from Brazil (Secchi and Fletcher, 2004). Leslie's matrix elements for each age classes: reproductive rates (m_j) and survival probabilities (p_j) are taken from specific studies from Argentina and Brazil. Then, fecundity (f_j) is estimated as a product: $m_j\ p_j$. All the compiled data information is presented in Section 2.2. The Franciscana dolphin's lifespan seems to be around 20 years (Pinedo and Hohn, 2000), the oldest aged dolphin was a female of 21 years (Pinedo and Hohn, 2000) and a male 20 years old (Silva et al., 2020). However, only a small percentage of the animals live more than 13 years regardless of their geographic location (Kasuya and Brownell, 1979; Pinedo and Hohn, 2000; Di Beneditto and Ramos, 2001). In previous life history studies of Franciscana from Argentina, the maximum age reported was a 13-year old male. Furthermore, over 60% of entangled individuals were under 4 years of age (Negri et al., 2014). In accordance with the age at first reproduction (AFR) and the maximum age reported for Argentina (Panebianco, 2011; Negri et al., 2014; Panebianco et al., 2016) a 14×14 Leslie's matrix was structured considering calves (ages 0 to 3) and non-calves (individuals of 4 to 13 years of age). Here, we consider that survival probabilities are modified by (random) incidental mortality in addition to its natural dependence. Data on the age–frequency distribution of Franciscanas bycatch off Argentina (Negri et al., 2013) were adopted for the incidental mean-value mortality characterization.

It is worth mentioning that the present work shows an applicability procedure to deal with the complex problem of the time-evolution using a recurrence relation of the Leslie (birth-pulse) type. However, the result of an effective λ_{eff} (Perron–Frobenius eigenvalue) strongly depends on the assumption of the type of distribution and correlations among the demographic parameters in a random matrix approach. Our task here is to give results for modelling the population growth of the Franciscana dolphin by calculating the growth rate in a mean-value approximation. This analysis will help promote further studies to understand age-structured time-dependent dynamical behaviour associated to wild populations at risk.

2.2. Vital parameters in Leslie's Matrix Model

Leslie's matrix elements are positive numbers that frequently can be assumed to have random contributions to represent the uncertainties in vital parameters. Then, the matrix **M** in Eq. (1) has the structure:

$$\mathbf{M} = \begin{pmatrix} m_0p_0 & m_1p_1 & \dots & m_{12}p_{12} & m_{13}p_{13} \\ p_0 & 0 & & 0 & 0 \\ & \vdots & \ddots & & \vdots \\ 0 & 0 & p_{12} & \cdots & 0 \end{pmatrix}$$

where m_j p_j >0 are fecundities f_j (then m_j are reproductive rates) and $0 < p_j < 1$ are survival likelihood for each age-class $j = 0, 1, 2, \ldots 13$.

Taking into account that survival parameters p_j may have random contributions, we can approximate fecundities by: $f_j = m_j\rho_j$, where ρ_j is a mean-value survival probability and then we get:

$$\mathbf{H} = \begin{pmatrix} f_0 & f_1 & \cdots & f_{12} & f_{13} \\ \rho_j & 0 & & 0 & 0 \\ & \vdots & \ddots & \vdots & \\ 0 & 0 & \rho_{12} & \cdots & 0 \end{pmatrix}$$

Using this matrix **H** is the simplest approximation that we could do to work out the random problem. Therefore, matrix **H** will reproduce the familiar result from a mean-value Leslie's dynamic, *i.e.*, the growth rate of population is given by the positive eigenvalue of matrix **H**; which is, the Perron–Frobenius eigenvalue $\lambda > 0$ (Cáceres, 2017). This eigenvalue corresponds to the maximum positive root of the polynomial: $P(\lambda) = det\,|\mathbf{H} - \lambda 1|$ where **1** is the identity matrix of dimension 14×14. Using Leslie's matrix **H** in the expression for the polynomial $P(\lambda)$ we get:

$$P(\lambda) = 1 - \prod_{l=1}^{14} \frac{1}{\lambda^l} \frac{f_{l-1}}{\rho_{l-1}} (\rho_0\rho_1 \ldots \rho_{l-1}) \tag{2}$$

The correspondence between Lotka's growth rate r and the mentioned Perron–Frobenius eigenvalue is given by: $\lambda = e^r$. The age-specific reproductive rate $m(x)$, fertility $f(x)$, and survival probability $\rho(x)$ are connected by formula $m(x)=f(x)/\rho(x)$, then it follows

$$l(x) = \prod_{j=1}^{x} \rho_{j-1}$$

for an animal surviving the length of time from 0 to age x. Then, Eq. (2) reduces to the continuous-time Lotka formula for the growth rate r, that is:

$$1 = \sum_{x=1}^{14} e^{-rx} m(x)\, l(x)$$

Addressing the Leslie approach is also useful when using a matrix theory for an age representation where random number can be handled by perturbation (Cáceres and Cáceres-Saez, 2011). In particular, a generalized polynomial $P(\lambda)$ has been written as a function of the random perturbations. This allows finding the effective eigenvalue λ_{eff} (Cáceres and Cáceres-Saez, 2013). The first approximation for the calculation of the Perron–Frobenius eigenvalue corresponds to $\lambda(\mathbf{H})$ and it is in accordance with the use of Leslie's matrix $\mathbf{H} = \langle \mathbf{M} \rangle$. Therefore, the growth rate can easily be calculated from Eq. (2) using Mathematica 5.2 software (assuring a large number of digits). These results will be presented in the next sections.

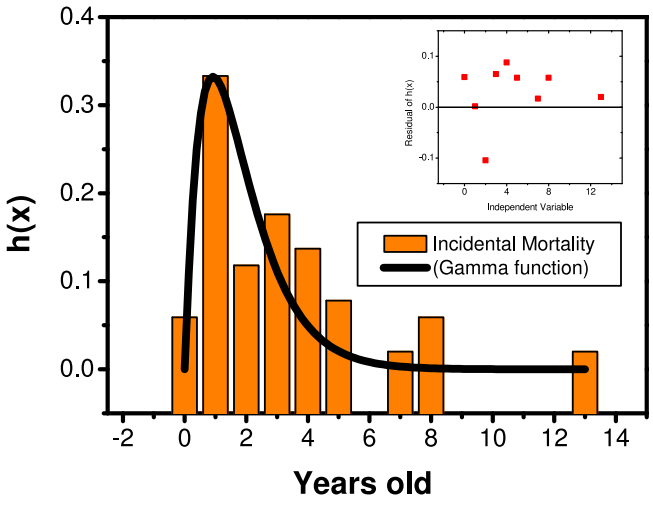

Fig. 1. Age–frequency distribution of bycatch Franciscana dolphins, Argentina between 2003–2009 (Negri et al., 2014). The line represents the best fitting through a Gamma distribution (statistical parameters of the fitting incidental mortality analysis are presented in Table 4).

Table 1
Survival rate of Franciscana dolphins by Secchi and Fletcher (2004).

Survival parameters $S_j = 1 - n_j$	Age classification j
$n_0 = n_1 = 0.1$	0, 1
$n_2 = n_3 = n_4 = n_5 = 0.09$	2, 3, 4, 5
$n_6 = 0.10$	6
$n_7 = 0.12$	7
$n_8 = 0.14$	8
$n_9 = 0.16$	9
$n_{10} = 0.20$	10
$n_{11} = 0.25$	11
$n_{12} = 0.31$	12
$n_{13} = 0.38$	13

Table 2
Franciscana dolphin life history parameters.

Vital parameters	Age classification
$m_0 = m_1 = m_2 = m_3 = 0$	Null birth rate for age classes 0, 1, 2, 3
$m_4 = 0.20$	Age-specific birth rate class 4
$m_5 = 0.335$	Age-specific birth rate class 5
$m_j = 0.25$	Age-specific birth rate classes $6 \leq j \leq 13$
$p_0 = (1 - \Delta)(1 - n_0)$	Total 0 - age survival probability
$p_j = (1 - h_j)(1 - n_j)$	Total survival probability for $j \geq 1$
$f_j = m_j p_j$	Age-specific fertility

2.3. The Franciscana Life History Parameters

Tables 1 and 2 of life history parameters were created using biological data reported in previous studies (Secchi, 2006; Panebianco et al., 2012). We estimated the ASM (Attainment of Sexual Maturity) to be 4.05 years using the De Master Method (Panebianco, 2011; Panebianco et al., 2016). Thus, given a gestation length of about 11 months, the AFR would be around 4.9 years. It has been indicated that vulnerability of population does not depend on sex, therefore, the sex ratio at birth (SR) is expressed as the proportion of females to the total number of adult individuals for the whole life cycle. Among marine mammals the SR estimation by direct observations is often skewed due to space–time variability of sexual segregation (Perrin and Reilly, 1984). Following Fifas et al. (1998), this issue does not invalidate the hypothesis of an equivalent presence of both sexes in populations; therefore, SR value is fixed at 0.5. The reproductive rates $\{m_j\}$ are presented in Table 2 from collected data from Argentina, and in Fig. 1 we show data of the incidental

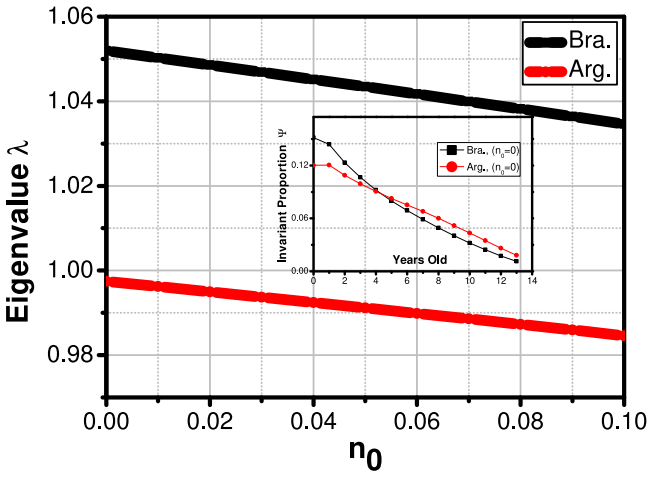

Fig. 2. Growth rate λ (Perron–Frobenius eigenvalue) as a function of calf natural mortality $n_0$considering birth rates of Franciscanas from Argentina and Brazil without incidental mortality. The calf natural mortality range for 0-age (model-parameter) is $n_0 \in [0, 0.1]$. The inset shows the comparison of the corresponding invariant proportions (Perron–Frobenius eigenvectors) in case $n_0 = 0$.

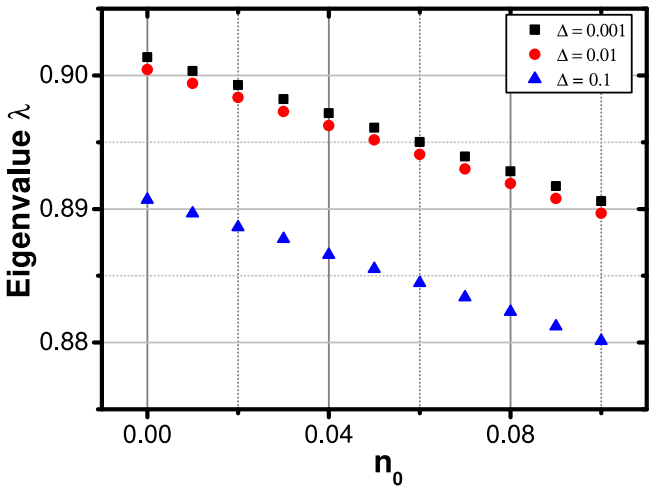

Fig. 3. Growth rate λ (Perron–Frobenius eigenvalue) as a function of calf natural mortality n_0 for three values of $\Delta \equiv h_0$, considering birth rates of Franciscanas from Argentina. Increasing values of Δ from the top to the bottom. The range of the model-parameter is $n_0 \in [0, 0.1]$.

mortality $\{h_j\}$ (Negri et al., 2013, 2014). Noting that incidental mortality h_0 could have a questionable value from the best fitting of data (predicting $h_0 = 0$), we will model it by a set of values $\Delta = h_0 = (0, 0.001, 0.01, 0.1, 0.2)$. In addition, the natural mortality, n_j, will be modelled using the estimation of survival rates of Franciscana by fitting Siler's model on age-at-death of beachcast and bycatch following Secchi and Fletcher (2004) and Secchi (2006) (see Table 1).

Then considering that the survival probability accounts for the independent effects of natural and incidental mortality, we can estimate that the total survival probability is given by:

$p_j = (1 - h_j)(1 - n_j)$ in Table 2

In Table 2, h_j is the incidental mortality which will be taken $\langle h_j \rangle$, in the mean-value of bycatch data from Argentina and n_j the natural mortality variable for age $j > 0$ from Brazil. The values for the incidental mortality $\langle h_j \rangle$ derived from a data series available in Negri et al. (2013) (Fig. 2), after interpolating the age-data from an empirical function with the best correlation coefficient (R), and testing the goodness of fit test (Null-Hypothesis test using OriginPro 7.5 software). The natural survival rate $1\text{-}n_0$ of Franciscana is in fact unknown, and for individuals of age $j > 0$ the natural mortality $n_{j>0}$ was estimated from age-at-death of bycatch individuals, after careful treatment (Secchi and Fletcher, 2004). We remark that considering incidental mortality reduces the life span of individuals in the population; then, it would be important to introduce a systematic analysis traced by this modification.

3. Results and discussion

3.1. Natural birth rate and comparative growth rates

We give an estimation of the growth rate λ of Franciscana dolphin in Argentina by using the natural survival, n_j from derived data of Brazil. This assumption was also employed in other cetacean studies such as the harbour porpoise (*Phocoena phocoena*) (Cáceres and Cáceres-Saez, 2011). Usually, some parameters in life tables are extrapolated from other mammal species with similar life histories as an alternative assumption and when no species-specific data are available to estimate the survival rate (Woodley and Read, 1991). Consequently, we first report a comparative analysis of the growth rate λ using natural survival parameters (Table 1) and the birth rate (Table 2). For completeness, here we have summarized birth rate data from Brazil and Argentina in Table 3. As noted by Danilewicz (2003) in Brazil, the sexual maturity in females is attained between 2 and 5 years of age, and the estimation of the mean age at sexual maturity in southern Brazil was calculated as 3.7 years (CI 95% = 3.0–4.4 years). Due to the small sample size this was not assessed, however, Table 3 denotes that there must be a shift to older years for the mean age of sexual maturity in Argentina. Fig. 2 shows the dolphin growth rate $\lambda = \lambda(n_0)$ for Argentina and Brazil (using the same natural mortality n_j from Table 1), and the inset shows the corresponding invariant eigenvectors for the case: $n_0 = 0$ (which corresponds to Perron–Frobenius eigen-problem analysis in accordance with the time evolution of population vector state $\mathbf{X}(m)$ using Leslie's recurrence relation without incidental mortality, i.e., we have used $h_j = 0$ for all j). The estimated growth rate λ shows that Franciscana dolphins in Argentina may be under severe threat.

Table 3
Franciscana dolphin birth rates from Argentina and Brazil.

Birth rate estimated for Argentina	Birth rate estimated for Brazil
AFR ∼ 4	AFR ∼ 3
$m_j = 0$, {j = 0, 1, 2 }	$m_j = 0$, {j = 0, 1, 2}
$m_3 = 0$	$m_3 = 0.315$
$m_4 = 0.20$	$m_4 = 0.50$
$m_5 = 0.335$	$m_5 = 0.335$
$m_6 = 0.25$	$m_6 = 0.5$
$m_j = 0.25$, {j = 7, 8, . . . , 13}	$m_j = 0.165$, {j = 7, 8, . . . , 13}

Table 4
Statistical indices for the fit of incidental mortalities data of Franciscana dolphins from Argentina.

Statistical indices	Gamma function: $x^A e^{-Bx}$
A	1.01858
B	1.10498
$\frac{\chi^2}{DOF}$	0.00479
Correlation coefficient R-square (R)	0.504
Residual sum of squares (SSR)	0.03354
Degrees of freedom (DOF)	7
Fit status succeeded (number of iterations)	100

3.2. Age-dependent incidental mortality data

The vital parameters in the (mean-value) Leslie's matrix **H** were written considering that the survival probability accounts for the independent effects of natural and incidental mortality: $\rho_j = (1 - \langle h_j \rangle)(1 - n_j)$. The mean-values $\langle h_j \rangle$ can be obtained from Fig. 1, after fitting the collected data h_j with an empirical function in order to achieve a complete age-structure data set (j=0,1,2,3,…,13) in **H**. All statistical parameters indicating the goodness of fit test (Null-Hypothesis testing) associated to the Gamma function in Fig. 1 are presented in Table 4.

As noted through bycatch data from Argentina (Fig. 1, in the surveyed period between 2003–2009), about 74% of these entangled animals were sexually immature (Negri et al., 2013). Despite uncertainty due to small sample size, the mean age of mature and immature females was estimated at 6.25 (SD 2.06) and 2.06 (SD 1.52), respectively. These numbers also show the same tendency to older years for sexual maturity (a shift compared with results of Brazil) as commented above from the birth rate data of Argentina (see Table 3).

The age-structured data for the incidental mortality is summarized in Fig. 1 and the fitting (line) Gamma function is summarized in Table 4. An interesting outcome reporting the threat and correlations to these data points is the annual total number (ATN) of bycatch, which is calculated as: ATN = 112.14 (95% CI: 92.22–134.77) in the period years from 2006 to 2007, and ATN = 64.45 (95% CI: 50.17–82.85) between the years 2007–2008. According to Negri et al. (2013), these confidence intervals may indicate that data of Fig. 1 should be used considering an error around 30%.

3.3. Growth rate using incidental mortality in mean-value

In this section, we analysed the growth rates λ of the Franciscana dolphin population as a function of natural mortality n_0 (natural survival: $S_0 = 1 - n_0$) and considering a set of values for the incidental mortality factor ($\Delta = h_0$) for 0 age (neonates). Fig. 3, shows $\lambda = \lambda(n_0)$ for three values of Δ using mean values $\langle h_j \rangle$ from the collected data. This analysis corresponds to the growth rate λ in accordance with the time-evolution of the population vector state $\mathbf{X}(m)$ using Leslie's matrix procedure. It can be noted, that unless we enlarge the data collection of incidental mortality, we will not be able to introduce the random Leslie approach, because to do this analysis we would need to know statistical moments of collected data or use some empirical probability distribution for the values h_j.

The response or functional behaviour of $\lambda = \lambda(n_0)$ is <1 and almost a linear function of n_0. In fact, this linearity is a consequence of the small variation of the survival age-structure $1 - n_j$. For values of $\Delta = \{0.001, 0.01\}$ the difference in the plot $\lambda = \lambda(n_0)$ is not so large. It is important to note that even without the incidental mortality, our results point out that λ is <1 for any value of the natural mortality rates $0 < n_0 < 0.1$ (see Fig. 2). For $\Delta = 0.1$ (which is a reasonable value for the incidental mortality in calves aged *0*-year old). Overall, these results may indicate a severe risk for the species in the marine coastal area of Argentina. A better estimate of growth rate, considering the distribution of incidental mortality parameters, can be obtained if bycatch data are improved (Cáceres and Cáceres-Saez, 2011).

3.4. Invariant proportion population analysis

The estimation of λ is associated to the evolution of the vector state considering the age structure of population (Leslie recurrence relation), so it is also possible to calculate the invariant proportion of population in a consistent way (Perron–Frobenius invariant vector state Ψ). Similar estimations have been reported

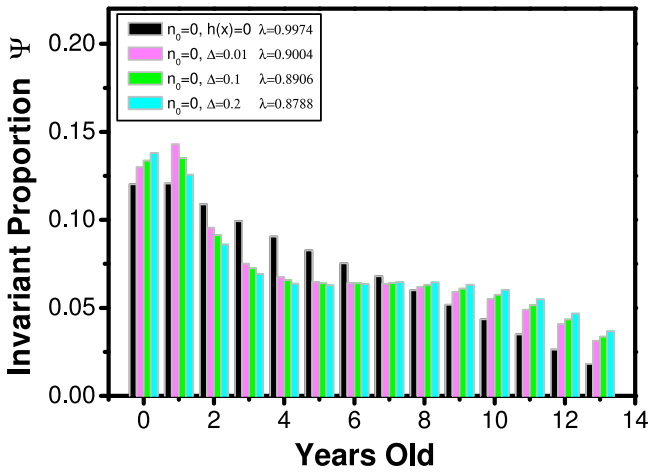

Fig. 4. The invariant population vector state Ψ is represented for three values of $\Delta \equiv h_0$, in the case when $n_0 = 0$. The black columns correspond to the case without incidental mortality (as in Fig. 2). The corresponding values of growth rate λ are presented in the inset. (For interpretation of the colour in this figure, the reader is referred to the web version of the article).

in the past for other small cetaceans (Woodley and Read, 1991; Cáceres and Cáceres-Saez, 2013; Hashimoto et al., 2013). In Fig. 4, we presented the invariant age-structure population of Franciscana dolphin, for different values of the parameter Δ, in order to compare with the frequency of bycatch in Argentina. Also, Fig. 4 shows the invariant population vector state Ψ (using the calf natural mortality value $n_0 = 0$) for a set of three values of incidental mortality for *0*-age Δ = (0.01,0.1,0.2). We present these results as column plots to highlight its peculiar structure. We can compare this age-structure with the one associated to the case with zero incidental mortality (in this case, black columns are monotonically decreasing), thus, we realize that considering incidental mortality the invariant vector has an age structure similar to the one from the frequency of bycatch (Fig. 1). This may indicate that the age-structure in the frequency of bycatch is more related to the stable population than to a social behaviour of the species. In addition, we can also see that the structure of Ψ for different values of Δ shows an "inversion-point" at a typical age value (in this case around 6 years old). This indicates that the fine structure of the invariant vector depends on the distribution $h(x)$ associated to the incidental mortality. To quantify the global survival probability we can calculate the mean survival probability $\langle S \rangle$ associated to the invariant proportion:

$$\langle S \rangle = \sum_{j=0}^{13} (1 - n_j)\Psi_j$$

here, n_j comes from Table 1 and Ψ_j is the j-th component of the invariant vector state, i.e., the j-stage proportion of the stable population. The value of $\langle S \rangle < 1$ is sometimes of relevance to established criteria on species at risk of extinction. Nevertheless, we note that these values may be quite similar if the difference between λ is small. Table 5 shows values of the mean survival probability $\langle S \rangle$ for the three different eigenvalues λ < 1 associated to Fig. 4 (in Table 5, λ = 0.9974 corresponds to the zero incidental mortality case).

The calculation of the Perron–Frobenius eigenvalue λ and eigenvector Ψ were made using the Mathematica 5.2 software assuring a large number of digits (larger than 10^{-10}), that is why we kept (numerically) various digits after zero in Table 5. A different task is to calculate the CI for the eigenvalue, or for the survival probability <S>. As stated above, we do not have

Table 5
Mean survival probabilities <S> contrasted for several values of $\lambda < 1$ (in correspondence with Fig. 4).

Mean	$\lambda = 0.9974$	$\lambda = 0.9004$	$\lambda = 0.8906$	$\lambda = 0.8788$
<S>	0,8767	0,8656	0,8634	0,8608

access to the corresponding CI for each element of the Leslie's matrix, so we cannot calculate an associated CI for the Perron–Frobenius eigenvalue λ. Nevertheless, according to the data we have used, we could assume that these elements may have an error of ±30%, and therefore, it is possible to estimate an error to the positive eigenvalue λ. Considering random independent errors in the elements of the matrix, we have run many numerical evaluations for the eigenvalue and reached to the conclusion that the error in λ would be of the order of ±3%. In fact, considering an (independent) error of ±30% in each value of the incidental mortality, i.e., $h_j \pm 30\%$, this fact leads to a variation in the value of λ, which in the worst case is of the order ±1.9%. On the other hand, considering an error of ±30% in values of the birth rate ($m_j \pm 30\%$), these errors will lead to a variation in the value of λ which in the worst case scenario is around ±2.28%. So, we can assume that all present numbers for the eigenvalues should be considered with an error of ±3% in Table 5. Incorporating a more accurate age-structure into the survival probabilities would give valuable results for the invariant proportion of the Franciscana dolphin population. This type of Leslie analysis may help to estimate the state of a wild population under vulnerability. Given the uncertainty of this population modelling approach, a potential for growth rates below one (λ<1) indicates a plausible threat to the survival and population viability of the Franciscana under the ongoing bycatch mortality level at their southernmost distribution in Argentina. In consequence, the estimated population parameter as obtained here should be suitable for integrating conservation plans for the regional marine ecosystem.

3.5. Enlarged Leslie's matrices and random variables

Models of population growth have many implications for management and conservation. The present analysis applies to the Argentina coastal marine system and could be extended to the wider Southwestern Atlantic Ocean. This method would reduce to a partitioned Leslie's approach where self-consistent approximations (for migrations) may be used to improve the present results. This mathematical modification would reduce to the use of enlarged Leslie matrices with inter-region spatial locations (Cáceres, 2017). A more exhaustive analyses using probability distributions for the elements and correlated random variables to characterize the implication on the incidental mortality h_j could also be used within the framework of a random Leslie matrix approach to calculate the effective growth rate λ_{eff} if we had a better field data collection (Cáceres and Cáceres-Saez, 2013).

4. Conclusions

The long-time asymptotic behaviour of the Franciscana population in Argentina has been characterized using the Leslie analysis in mean-value. The growth rate λ has been calculated as a function of the *0*-age calf natural mortality n_0, including the mean-value incidental mortality and using fecundity rates and natural age-dependent survival probabilities from studies from Brazil (until now the only source of information for this vital parameter available for the species). The calculation of the invariant proportion population (the vector state Ψ) and the mean survival probability $\langle S \rangle$ have been developed within Leslie's recurrence relation framework. The time evolution for the average of Leslie's vector population has been used to calculate growth rate of Franciscana dolphins from the South Atlantic Ocean.

We have performed the calculation of λ in terms of a mean-value Leslie's matrix **H** to estimate the growth rate considering incidental mortality in mean-value. Our task was to estimate λ as a function of natural mortality n_0 for several values of incidental mortality at *0*-age $\Delta = h_0$. We have followed the estimates for this species population proportions under bycatch, in particular the lower and upper limits of Δ may be questionable values as used. That is why we run the calculations for several reasonable values of Δ. We have shown that considering age-dependent values for the incidental mortality leads to drastic conclusions regarding the growth rate of Franciscana dolphins. In addition, we showed that the potential growth rates λ <1, which indicates a possible threat to the species in the sense of the population will not be stable under current incidental mortality levels at their southern distribution in South America. Overall, our analysis suggests that this population may not sustain such levels of bycatch under the survival probability estimates for the species, and our results are also critical in the sense that the dynamics of the vector state indicates that only a dramatic decline in mortality, would allow the population to withstand the present incidental mortality pressure. Although there are national and provincial laws in Argentina protecting cetaceans as well as other marine mammals, there is no framework that integrates the regulation of marine and coastal development regarding marine mammal preservation. Under the precautionary principles in conservation and environmental science strategies, the data generated through this study should be considered as a tool for implementing and addressing the impact of fisheries on this and other coastal marine species in Argentina.

CRediT authorship contribution statement

Manuel O. Cáceres: Conceived and designed of the study, Performed the analytical equations, Analyzed the data, Wrote the paper. **Iris Cáceres-Saez:** Conceived and designed of the study, Analyzed the data, Data collection, Analysis tools, Critical contributions, Wrote the paper. **Eduardo R. Secchi:** Analyzed the data, Data collection, Analysis tools, Critical contributions. **M. Fernanda Negri:** Data collection, Analysis tools, Critical contributions. **M. Victoria Panebianco:** Analyzed the data, Data collection, Analysis tools, Critical contributions. **H. Luis Cappozzo:** Analyzed the data, Data collection, Analysis tools, Critical contributions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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