Estimating survival rates of franciscana by fitting the Siler model to data on age-at-death of beachcast and bycatch and by a modelling approach using life tables of similar species: a comparison

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Abstract

For cetaceans, survival has been estimated from several different types of data, including a) age-distribution of catch data during commercial whaling; b) age-distribution of animals killed in drive fishery; c) individual based mark-recapture models of photo-identified animals; d) using a range of life tables of several species with similar life histories; and e) fitting Siler (1979) competing-risk models to age-at-death data. All these approaches rely on assumptions that, in many cases, are difficult to satisfy. For several reasons the use of mark-recapture techniques is unsuitable for franciscana. Age distribution data of bycatch has not been used so far for any cetacean species because of the unequal vulnerability of different age classes. Beachcast data are typically biased, as naturally-killed dolphins and bycatch are mixed in unknown proportions. In this study we developed a method that combines age distribution data of bycatch and beachcast animals to identify and adjust the bias. Once the bias is adjusted, the age distribution data were fitted by the Siler model and survival rates of franciscana were estimated. Results were compared to those obtained from an alternative approach of using life tables from similar species to estimate survival rates of franciscana. The two methods resulted in identical mean survival rates for juvenile franciscana (*i.e.* 0.91 and 0.90). The values for adults were also identical when the age-at-death data was truncated at age 14 (*i.e.* 0.854 and 0.86). This suggests that bycatch age-at-death data, after careful treatment to reduce bias effects, may be useful to estimate approximate survival rates.

Keywords: Survival rates, Siler model, model life tables, age distribution.

Introduction

In long lived mammals, bird and reptiles, survival rate (especially of adult females) is the parameter to which measures of population performance are most sensitive. Hence it is the most relevant parameter for demographic studies (Burgman *et al.,* 1993, Caswell, 2001; Morris and Doak, 2003) and for understanding evolutionary details of the species' life history (Caughley, 1977; Western and Ssemakula, 1982; Millar and Zammuto, 1983).

It follows that survival should be estimated well, especially for demographic and viability analyses where it plays a major role in the predictive power of the analyses.

Unfortunately, estimating survival rates that are free of bias or assumptions is difficult for long-lived species (*e.g.* Eberhardt, 1985). For cetaceans, survival has been estimated from several different types of data, including a) age-distribution of catch data during commercial whaling (*e.g.* Ohsumi *et al.*, 1970; Ohsumi and Masaki, 1975); b) age-distribution of animals killed in drive fishery (Kasuya and Marsh, 1984); c) individual based mark-recapture models of photo-identified animals (see several articles in Hammond *et al.*, 1990; Cameron *et al.*, 1999); d) using a range of life tables of several species with similar life histories (*e.g.* Barlow and Boveng, 1991; Caswell *et al.*, 1998; Secchi, 1999); and e) fitting Siler (1979) competing-risk models to age-at-death data (Stolen and Barlow, 2003). Age distribution data of bycatch has not been used so far for any cetacean species because of the unequal vulnerability of different age classes. All these approaches rely on assumptions that, in many cases, are difficult to satisfy.

The first two approaches assume that age determination is accurate, that the sample of aged animals is unbiased, and that the population has a stable age structure. For example, estimating, the age of baleen whales is very difficult due to a lack of calibration methods. For toothed cetaceans age estimation has been studied more intensively (*e.g.* Perrin and Myrick, 1980) but the precision varies between species, according to the technique employed and generally decreases for older individuals (Hohn and Fernandez, 1999). Commercial catch tends to be biased toward larger, possibly older, animals due to their higher economical value (Tønnessen and Johnsen, 1982) whilst incidental capture is often biased towards young individuals due to their higher vulnerability (*e.g.* Perrin *et al.*, 1994). Exploited populations are unlikely to have a stable age structure if the impacting source affects the age classes differently from year to year. For age distribution to be stable, age-specific differences in both death rates and birth rates across age classes must be constant, and need to have been so long enough for the age structure to equilibrate.

Survival rates of several cetacean species have been estimated with capture-recapture analysis of photo-identification data. Individuals belonging to different gender or age and/or stage classes are not distinguished in the field. For some species (*e.g.* Hector's dolphins), a female can only be distinguished from a male when accompanied by her calf. In such situations individuals of several ages need to be pooled into a few stage classes, with no division by gender. If the proportion of sampled animals does not equal the proportion in the population, estimates will be biased. For instance, if, for any reason

(*e.g.* gender or age-related dispersion) individuals representing a certain age class move from the area, the estimation of survival for this class will be underestimated. The potential for this sort of problem may be minimised via large sample sizes, and careful survey design (*e.g.* Fletcher *et al.,* 2002). However, yet another problem remains. This approach implicitly leads to estimation of an average mortality rate within a stage class. This may affect the resulting population projections and have significant conservation implications. The magnitude of these errors varies among species and depends upon their life-history and on patterns of human-related mortality. If juveniles (all immature non-calves) are more vulnerable to bycatch in fisheries than adults (as is the case for many small cetacean species, *e.g.,* Hector's dolphins - Dawson, 1991; harbour porpoises - Read and Hohn, 1995; franciscana - Secchi *et al.,* 2003) then survival rates estimated using mark-recapture techniques of photo-identified dolphins which consider bycatch and natural mortality together will underestimate survival rates of adults (the less vulnerable age class) to an extent that depends on the amount of data coming from the vulnerable age class. Also, there might be differential vulnerability among adults, with one sex being more prone to bycatch than the other. Males are, generally, less philopatric than females in several cetacean species (*e.g.* bottlenose dolphins – Scott *et al.*, 1990; beluga whales – O'Corry-Crowe, 1997; Dall's porpoise – Scorza-Trevino and Dizon, 2000) making them potentially more likely to have fatal encounters with nets. This is especially true in areas where nets are more common outside the population's preferred sites. These differences, when possible, must be taken into account to minimise biases in survival rate estimates.

The use of model life tables derived from other mammals with similar life histories is another alternative when no species-specific data are available to estimate survival rate. One potential problem is that life history traits might be correlated. For example, low costs of reproduction (*e.g.* wide inter-birth intervals) might affect life expectancy (both juvenile and adult survival rates) and age at first reproduction. When a broad range of correlated life histories are assumed to be independent in estimating survival rates, either unfeasibly low or unfeasibly high rates can be obtained. Appropriate truncation of the distribution could provide reasonable results but the associated uncertainty could be of such magnitude that the estimated parameter would be difficult to interpret. Possible ways to correct this problem include restricting the surrogate species to those with life histories that closely match the species studied. This basically ensures that random values are drawn from a more limited range so that the assumption of independence of parameters becomes less likely to result in an unrealistic range of values for survival rate. For

example, there is strong evidence for mammals and birds that body mass is positively correlated with survival (*e.g.* Milar and Zammuto, 1983; Krementz *et al*., 1997). Hence, it is crucial that selected model species have a body mass as similar as possible to the species under study.

The assumptions associated with each of those methods are often not satisfied and the ideal scenario of bias-free estimation will rarely be met. Given that these are the only options available to estimate survival rate for cetacean species and given also the relevance of this estimate, any of the methods that suits the available data should be tested. However, the caveats and assumptions associated with the selected method should always be clearly stated and the consequences of unsatisfied assumptions evaluated. Mark-recapture of individually identified animals is possibly the most reliable of the above methods because it is based on following the fate of individuals, potential biases (*e.g.* individuals with varying "capture-recapture" probabilities) can be overcome by careful model selection (White and Burnham, 1999), especially if sample size is large and representative in time and space.

Unfortunately, individual identification techniques are not suitable for many species. Franciscana has several behavioural and morphological characteristics that make it difficult to observe at sea (Bordino *et al.,* 2002). In southern Brazil, where bycatch rates are very high (Secchi *et al.,* 2003), no live franciscana have been seen in more than 150 boat surveys (GEMARS[1], pers. commn). The species seems boat-negative along most of its range (Bordino *et al.,* 2002). They spend little time (about 4%) at the surface and surface inconspicuously (Bordino *et al.,* 1999). A further complication is that franciscana are small (no longer than 1.7m) and coloured similarly to the turbid waters characteristic of much of their range. All these aspects make the use of mark-recapture techniques unsuitable. Of the methods mentioned above, the most promising for franciscana is analysis of age distribution of bycatch and beachcast animals. As mentioned above, beachcast data are typically biased, as naturally-killed dolphins and bycatch are mixed in unknown proportions. If a way to identify the bias and its magnitude could be found, the age distribution could be corrected and fitted by the Siler model. Potential differences in between this approach and the alternative of using life tables from other species will be investigated.

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The objectives of this study are to:

- Use available data on age-at-death from beachcast and bycatch to describe the mortality pattern of franciscana and estimate survival rates by fitting the Siler competing-risk model;

- Calculate the precision of these estimates;

- Determine a likely range of survivorship schedules for franciscana based on the life tables of mammals with very similar life history;

- Compare the estimates obtained by the two approaches and discuss their reliability in the context of modelling population growth and viability.

Methods and Modelling approach

The data

Age data from franciscana beachcast in southern Brazil (n=184) and by-caught off Uruguay (n=102) were obtained from the literature (Pinedo, 1994). Age distribution of bycatch in southern Brazil was estimated from individuals incidentally entangled in coastal gillnet fishery during 1994/97 (n=115). Animals were aged via counting the Growth Layer Groups (GLGs) in the dentine and cementum of longitudinal teeth sections (*e.g.* Kasuya and Brownell, 1979; Pinedo and Hohn, 2000). Each GLG represents one year in a franciscana (Pinedo and Hohn, 2000). Detailed descriptions of age determination in cetaceans can be found in Perrin and Myrick (1980) and, specifically for franciscana, in Kasuya and Brownell (1979) and Pinedo and Hohn (2000).

Fitting the Siler model to the data

The Siler model was chosen because it fits the expected mortality patterns of a wide range of long-lived species reasonably well (Siler, 1979). The model describes the general shape of the mortality curve using five parameters that account for an increasing risk of an individual dying at the beginning of life due to a period of adjustment to the environment, a constant risk through the whole life, and an increased risk due to senescence (see Siler, 1979 for details). Fitting the Siler model to cetacean age-at-death data was first attempted (for bottlenose dolphins) by Stolen and Barlow (2003). The authors assumed that the data were obtained from dolphins suffering natural mortality. For completeness, we give details about the method as follows:

Survivorship, the probability of living till age x, is expressed as the product of three competing risks, as defined in Siler (1979),

$$l(x) = l_j(x) \cdot l_c(x) \cdot l_s(x) \qquad \text{[eq. 1]}$$

where,

$$l_c(x) = \exp(-a_2 \cdot x) \qquad \text{[eq. 2]}$$

is a constant risk experienced by all ages,

$$l_j(x) = \exp\{(-a_1/b_1) \cdot [1-\exp(-b_1 \cdot x)]\} \qquad \text{[eq. 3]}$$

is an exponentially decreasing risk due to juvenile risk factors, and,

$$l_s(x) = \exp\{(a_3/b_3) \cdot [1-\exp(-b_3 \cdot x)]\} \qquad \text{[eq. 4]}$$

is an exponentially increasing risk due to senescent risk factors.

Age-specific survival rates (S_x) and mortality rates (q_x) are then obtained from,

$$S_x = 1-q_x = l(x+1)/l(x) \qquad \text{[eq. 5]}$$

Following the method of Stolen and Barlow (2003), the number of franciscanas dying in each age x (d_x) will be proportional to the number of franciscanas in that age times the mortality rate for that age (q_x).

$$d_x \propto \left[e^{-rx} \cdot l(x) \right] \cdot q_x \qquad \text{[eq. 6]}$$

Equation 6 is based on the assumption that the population is in equilibrium, with a growth rate r. A value of r needs to be chosen based on some prior assumptions (*e.g.*, $r=0$ if it is assumed that the population is stationary or $r>0$ if the population is suspected to be growing), then the Siler model is fitted to the data. Values of r between 0.02 and 0.04 are

assumed to be reasonable for impacted small cetaceans as these values are obtained using theoretical maximum reproductive rates (*e.g.* Reilly and Barlow, 1986; Wade, 1998). It is reasonable to assume that the franciscana population growth rate is greater than zero, as it has been killed in fisheries for a long period.

The probability, Pr(x), that an observed dead franciscana will be of age x is then

$$\Pr(x) = \frac{e^{-rx}\left[l(x) - l(x+1)\right]}{\sum_{y=0}^{w}\left\{e^{-rx}\left[l(y) - l(y+1)\right]\right\}} \qquad \text{[eq. 7]}$$

where w is the maximum observed age in the sample. The likelihood of an observed sample of age-at-death data is then

$$L(n_1, n_2, ..., n_w) = \prod_{x=0}^{w}\left[\Pr(x)\right]^{n_x} \quad \text{(Stolen and Barlow, 2003)} \qquad \text{[eq. 8]}$$
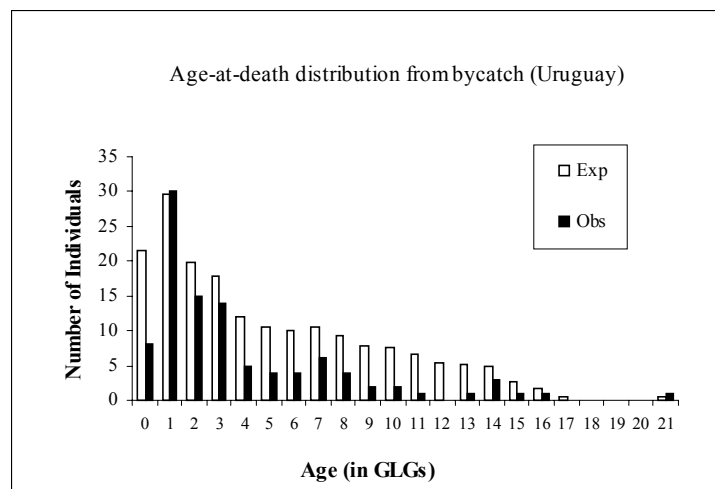
where n_x is the number of deaths observed at age x.

This model was fitted to the beachcast and bycatch age-at-death data by maximising the logarithm of the likelihood function using the Solver routine in Excel. In order to obtain standard errors of the parameter estimates, we used non-parametric bootstrap resampling.

Figure 1 shows that none of the various data sets fitted the model perfectly. Lack of fit is probably due to unequal vulnerability to entanglement across age classes. Although data exclusively from bycatch suggest a negative bias in the number of immature individuals (*i.e.* lower vulnerability), the beachcast data are only slightly positively biased in this class, but very positively biased in the age 13 class (Table 1). The high number of observed individuals in those ages could be due to the errors in age estimation. The pulp cavity in franciscana's teeth is filled approximately at age 5 (Kasuya and Brownell, 1979; Pinedo, 1991) making age estimation more difficult as age increases. It is more likely that a GLG will be missed than counting a layer that does not exist. Therefore, it is possible some individuals 13 years and older had their ages underestimated.

The best fit was to the beachcast data. We assumed that the expected age distribution obtained after fitting the Siler model to age-at-death from beachcast franciscana best described the age distribution of the franciscana population. Furthermore, because the aim of this study was to fit a model to the data in order to obtain survivorship estimates and to describe the mortality pattern of franciscana, the beachcast data were considered more appropriate as they are the only dataset containing individuals assumed to have died from natural causes. The pitfall of this approach is fitting a model to data that are a combination of bycatch and non-bycatch mortality.

While the Siler model provides a reasonable fit to age-at-death data from beachcast franciscana, we conducted a number of trials to improve the fit. For this assessment we set $r = 0.02$ because it is the midpoint between zero and the theoretical maximum value for a growing small cetacean population that was suggested by Reilly and Barlow (1986) and Wade (1998). The old age classes were pooled in order to better satisfy the assumption of the test, *i.e.* to ensure that the expected frequencies were all at least two (Harraway, 1993).
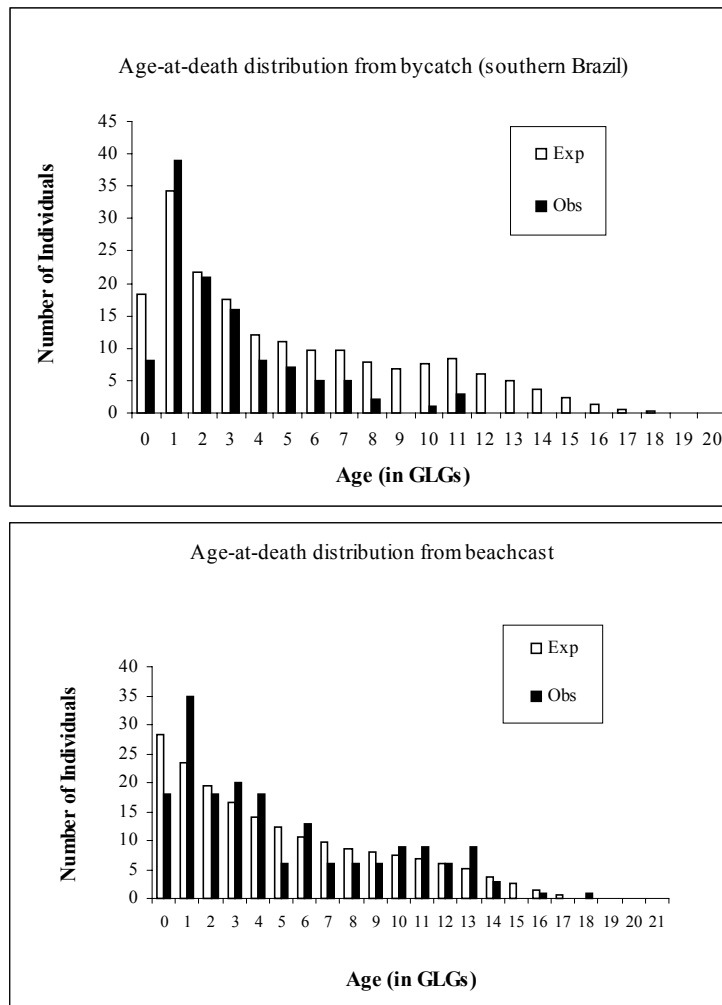
Figure 1. Observed and expected number of individuals in each age class from bycatch and beachcast data.

Table 1. Assessment of lack of fit of the Siler model to data on age-at-death from beachcast franciscanas. Chi-square (χ^2) values for each age x are shown in the last two columns. The value of r was fixed at 0.02. *lj, lc,* and *ls* are the three survivorship curves. Ages with high lack of fit are in bold. E: expected; O: observed; S: survival rate.

Pr	E	O	x	l	lj	lc	ls	S	χ^2	χ^2 (pooled)
0.15	28.2	18	0	1.00	1.0	1.0	1.0	0.86	**3.67**	**3.67**
0.13	23.3	35	1	0.86	0.9	1.0	1.0	0.86	**5.86**	**5.86**
0.11	19.5	18	2	0.75	0.8	1.0	1.0	0.87	0.11	0.11
0.09	16.4	20	3	0.65	0.7	1.0	1.0	0.87	0.77	0.77
0.08	14.0	18	4	0.56	0.6	1.0	1.0	0.87	1.12	1.12
0.07	12.2	6	5	0.49	0.5	1.0	0.9	0.86	**3.12**	**3.12**
0.06	10.7	13	6	0.42	0.5	1.0	0.9	0.86	0.49	0.49
0.05	9.6	6	7	0.36	0.4	1.0	0.9	0.85	1.34	1.34
0.05	8.7	6	8	0.31	0.4	1.0	0.8	0.84	0.84	0.84
0.04	8.0	6	9	0.26	0.3	1.0	0.8	0.82	0.51	0.51
0.04	7.4	9	10	0.21	0.3	1.0	0.7	0.79	0.35	0.35
0.04	6.8	9	11	0.17	0.3	1.0	0.6	0.75	0.74	0.74

0.03	6.0	6	12	0.12	0.2	1.0	0.5	0.70	0.00	0.00
0.03	5.0	9	13	0.09	0.2	1.0	0.4	0.63	**3.19**	**3.19**
0.02	3.8	3	14	0.05	0.2	1.0	0.3	0.55	0.17	0.17
0.01	2.5	0	15	0.03	0.2	1.0	0.2	0.45	2.48	1.36
0.01	1.3	1	16	0.01	0.2	1.0	0.1	0.34	0.07	
0.00	0.5	0	17	0.00	0.2	1.0	0.0	0.23	0.51	
0.00	0.1	1	18	0.00	0.1	1.0	0.0	0.14	5.67	
0.00	0.0	0	19	0.00	0.1	1.0	0.0	0.07	0.02	
0.00	0.0	0	20	0.00	0.1	1.0	0.0	0.02	0.00	
0.00	0.0	0	21	0.00	0.1	1.0	0.0	0.00	0.00	
								χ^2	31.04	23.63
								df	16	10
								P	0.013	0.009

A mixture model

Information on the age structure of the pure bycatch sample was used to separate bycatch and non-bycatch components of the beachcast data, and hence provide a better estimate of natural mortality. The probability of an animal of age x dying is a mixture of the probability of dying due to bycatch and due to natural mortality. The probability that an observed dead franciscana will be of age x is then assumed to be

$$\Pr(x)^* = \alpha \cdot \Pr(x) + (1-\alpha) \cdot Q(x) \qquad\qquad [\text{eq. 9}]$$

where $Q(x)$ is the probability that an observed dead franciscana that died from bycatch was in age x. We used the observed proportion of individuals in age class x present in the bycatch sample to estimate $Q(x)$; $\Pr(x)$ is the probability that an individual that has died from non-bycatch was in age class x, and α is the mixture parameter. α adjusts for differences between observed age structure from beachcast and the expected age structure after fitting the Siler model. For example, if the bycatch and the beachcast age-structures were identical, α would be zero. In such a situation, the age distribution of the bycatch would represent the age structure of the population, *i.e.*, bycatch would represent a random sample of the population. The greater the difference between the number of bycaught individuals of age x and the expected number in that age the higher the value of α needed for the model to fit. Figure 2 illustrates the predicted proportions of dead individuals in each age according to the Siler model fitted to the data after adjusting by the mixture parameter. The effect of adjustment is clearly noticeable in age 1.
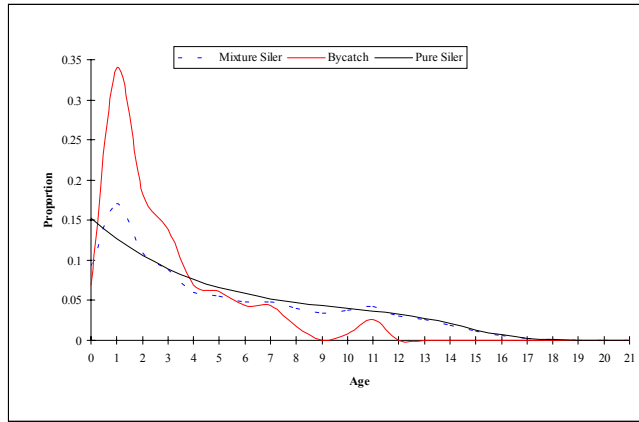
Figure 2. Predicted proportions of dead individuals in each age class according to Siler model fitted to beachcast data (black), to the proportion of each age class in the bycatch data sample (red), and to the Siler model fitted to the data after adjusting by the mixture parameter (dashed blue).

Only bycatch data from southern Brazil were used to estimate $Q(x)$ because they come from the same geographic location as the beachcast data. The method of Stolen and Barlow (2003) was modified to allow inclusion of the mixture parameter. The original five parameters and the mixture parameter α were estimated by maximising the logarithm of the likelihood function below, using the Solver routine in Excel.

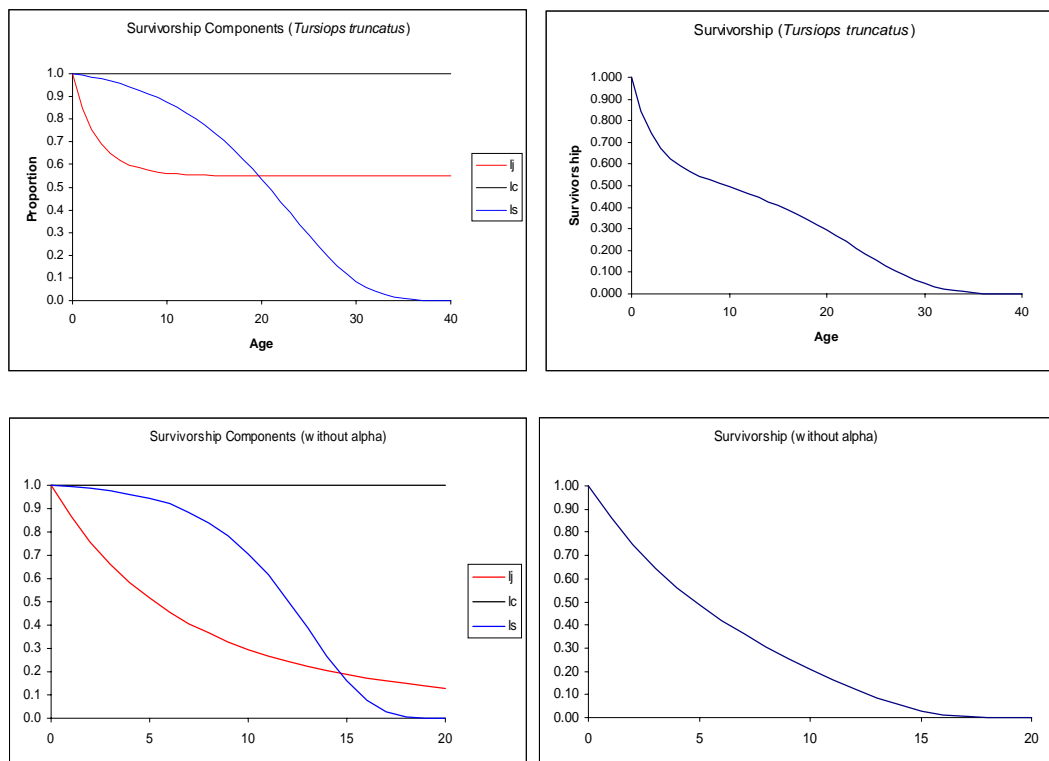$$L(n_1, n_2, ..., n_w) = \prod_{x=0}^{w} \left[\Pr(x)^* \right]^{n_x}$$ [eq. 10]

As we would expect, after using the mixture parameter approach a better fit of the model to the data was obtained. The estimate of α was 0.66. The χ^2 values are shown in Table 2.

Table 2. Assessment of lack of fit of the Siler model to data on age-at-death from beachcast franciscanas after adjusting with the mixture parameter α. Chi-square (χ^2) values for each age x are shown in the last columns. The value of r was fixed at 0.02. lj, lc, and ls are the three survivorship curves. E: expected; O: observed; S: survival rate.

Pr	Bycatch	E	O	x	l	lj	lc	ls	S	χ^2	χ^2 pooled
0.10	8	18.4	18	0	1.00	1.00	1.00	1.00	0.90	0.0	0.01
0.19	39	34.2	35	1	0.90	0.91	1.00	0.99	0.90	0.0	0.02
0.12	21	21.7	18	2	0.81	0.83	1.00	0.97	0.91	0.6	0.64
0.10	16	17.5	20	3	0.74	0.78	1.00	0.95	0.91	0.3	0.34
0.07	8	12.0	18	4	0.67	0.73	1.00	0.92	0.91	3.0	2.96
0.06	7	11.0	6	5	0.61	0.69	1.00	0.89	0.91	2.3	2.26
0.05	5	9.6	13	6	0.55	0.66	1.00	0.84	0.90	1.2	1.19
0.05	5	9.6	6	7	0.50	0.63	1.00	0.79	0.88	1.4	1.36
0.04	2	7.9	6	8	0.44	0.61	1.00	0.72	0.86	0.5	0.48
0.04	0	6.9	6	9	0.38	0.59	1.00	0.64	0.84	0.1	0.11
0.04	1	7.5	9	10	0.32	0.57	1.00	0.55	0.80	0.3	0.31
0.05	3	8.4	9	11	0.25	0.56	1.00	0.45	0.75	0.0	0.04

0.03	0	6.1	6	12	0.19	0.55	1.00	0.35	0.69	0.0	0.00
0.03	0	5.1	9	13	0.13	0.54	1.00	0.24	0.62	3.1	3.06
0.02	0	3.8	3	14	0.08	0.53	1.00	0.15	0.54	0.2	0.16
0.01	0	2.4	0	15	0.04	0.53	1.00	0.08	0.45	2.4	1.22
0.01	0	1.2	1	16	0.02	0.52	1.00	0.04	0.35	0.0	
0.00	0	0.5	0	17	0.01	0.51	1.00	0.01	0.25	0.5	
0.00	0	0.1	1	18	0.00	0.51	1.00	0.00	0.16	5.6	
0.00	0	0.0	0	19	0.00	0.51	1.00	0.00	0.09	0.0	
0.00	0	0.0	0	20	0.00	0.50	1.00	0.00	0.04	0.0	
0.00	0	0.0	0	21	0.00	0.50	1.00	0.00	0.00	0.0	
									χ^2	21.5	14.16
									df	15	9
									P	0.122	0.117

Bottlenose dolphins and franciscana are likely to have a similar pattern of natural mortality. Assuming that survivorship of bottlenose dolphins is well described by the method of Stolen and Barlow (2003), it might be expected that the mixture model curve for franciscana would be similar to the Stolen and Barlow curve for bottlenose dolphins. The mixture model indeed makes the curves more similar (Fig. 3), the only substantial difference being early in life. This is because calves are underrepresented in both bycatch and beachcast samples.
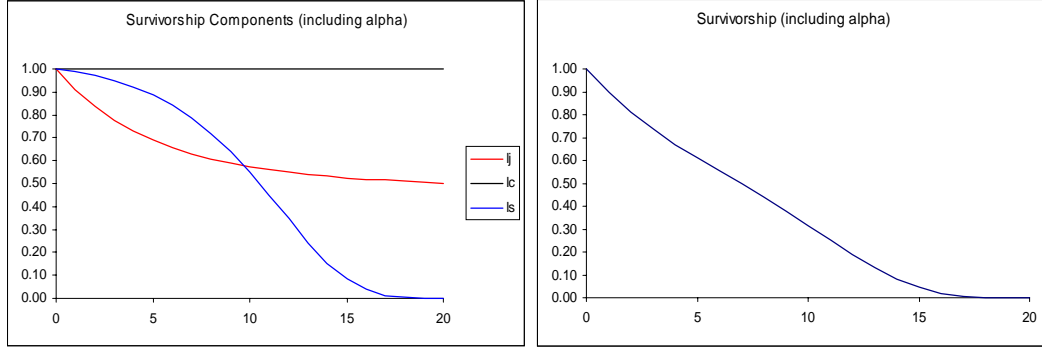
Figure 3. Survivorship components calculated by fitting Siler model to age-at-death data (first column) and survivorship curves (second column) for bottlenose dolphin (using data from Stolen and Barlow, 2003 - top), and for franciscana using data from beachcast only, without the mixture parameter α (middle) and with this parameter (bottom).

The model provided estimates of age-specific rates, from which we calculated stage-specific survival rates. These stage-specific estimates and their standard errors were used to model franciscana population dynamics in (Secchi and Fletcher, 2004: SC/56/SM20).

Estimation of the mean ($\overline{S}$) stage-specific survival rate for stage i was obtained using

$$\overline{S} = \sum_i W_i \cdot S_i \qquad\qquad [\text{eq. 11}]$$

$$W_i = \frac{e^{-rx} \cdot l(x)}{\sum e^{-rx} \cdot l(x)} \qquad \therefore \text{ for } i = 1, 2 \text{ and } 3 \qquad [\text{eq. 12}]$$

where the W_i give the stable stage distribution: If $i=1$ corresponds to calves ($x=0$); $i=2$ corresponds to juveniles [$x=1$ to age at first reproduction (AFR $\sim$ 4)]; $i=3$ corresponds to adults [$x=5$ to maximum observed age in the sample (19)].

Uncertainty in parameter estimates
The original data on bycatch and beachcast were resampled 5000 times using nonparametric bootstrapping (Manly, 1997). Each time the model was fitted to a new bootstrap sample, a new value of r was chosen from a uniform distribution between 0.02 and 0.04. This allowed for uncertainty in the true value of r for franciscana. These values

are within accepted thresholds of small cetacean population growth (*e.g.* Reily and Barlow, 1986; Wade, 1998). Variation in the assumed population growth rate affects the magnitude of the mortality rates but does not change the age-specific mortality patterns (Stolen and Barlow, 2003). Age-specific survivorship, mortality and stage-specific survival rates were calculated and stored for each of the bootstrap samples. In order to estimate the standard error of each estimate, we calculated the standard deviation of that estimate over all bootstrap samples.

The life-table model

This method consists of using survival schedules from other species (herein called model species) to represent franciscana's survival schedules. The survivorship curve is calculated using the equation:

$$l(x) = w_1l_1(x) + w_2l_2(x) + \ldots + w_5l_5(x) \qquad \text{[eq. 13]}$$

where x is age, $l_i(x)$ is the survivorship curve for species i, and the w_i are weights satisfying $w_1 + w_2 + \ldots + w_5 = 1$ and $0 \leq w_i \leq 1$ (i=1,2,…,5)

The survivorship curve of franciscana is expected to fall within the range of curves these species. The approach has been previously used by Barlow and Boveng (1991) to estimate population growth rate for spotted dolphins (*Stenella attenuata*) and maximum possible growth rate for harbour porpoise (*Phocoena phocoena*), and by Caswell *et al.,* (1998) to express uncertainty in population growth rate for harbour porpoises.

The method relies on the assumption that the model species and franciscana present similar life histories. Model species were selected from the literature. Unlike Caswell *et al*'s (1998) paper on harbour porpoise, we defined some criteria (aiming to be more rigorous on the concept of similar life history) prior to the selection of model species life tables. The criteria and rationale for choosing them are below:

a) Adult body mass cannot be more than one order higher or lower than franciscana's body mass (around 50kg - this is about the maximum observed body mass – pers. obs. of > 200 franciscanas incidentally killed in gillnet fisheries). Many life table traits are positively related to body size (*e.g.* age at maturity, generation length, life expectancy) while some are negatively related (*e.g.* litter size, reproductive value at maturity) (Millar

and Zammuto, 1983, Stearns, 1983). Millar and Zammuto found that a high proportion (about 76 to 82%) of the variation in the positively correlated variables is attributable to adult body mass. Body mass has been found to have a strong relationship to survival in many species of waterfowl (Krementz *et al.,* 1997) and other game birds in North America (Zammuto, 1986), the influence of body mass on survival being higher than geographic location or phylogeny.

b) Only monovular species are selected (*i.e.* litter size has to be one). Stearns (1976) suggested that reproductive rate (*e.g.* litter size) should be negatively correlated with adult survival.

c) Mean age of first reproduction (AFR) for the model species cannot be more than twice or less than half of franciscana's AFR (about 4.5 years – Danilewicz *et al.,* 2000; Danilewicz, 2003). Stearns (1976) and Millar and Zammuto (1983) provided evidence of positive correlation between age at maturity and life expectancy, and therefore survival (Pianka, 1978).

d) Calving interval should not be more than twice or less than half of franciscana's calving interval. Franciscana's calving interval varies from 1 to 2 according to the geographical location (*e.g.* Di Beneditto and Ramos, 2001; Rosas and Monteiro-Filho, 2002; Danilewicz, 2003). There is empirical evidence that shorter calving interval (higher reproductive rate) is associated with lower survival rate. This can be seen in a list of life traits of 50 mammal population available in the ESA's Electronic Data Archive: *Ecological Archives* E081-006.

e) Generation length should not be 50% more or less than the estimated value for franciscana (~ 8 years – Secchi and Wang, 2002). Generation length is a function of survivorship (Birch, 1948).

f) Maximum observed age should not to be more than twice or less than half of franciscana's maximum age (assumed to be around 20 years – Kasuya and Brownell, 1979; Pinedo and Hohn, 2000). Despite the limited value of using maximum age in life history analysis, mainly because of uncertainty in its estimation (Krementz *et al.,* 1989), this parameter is obviously related to survival in mammal species.

The first four traits discussed above are independent variables yet they vary together (Millar and Zammuto, 1983). The last two traits were used only as secondary criteria, aiming to increase rigour for the selection of model species.

A model species had to meet all these criteria to be selected. All selected species had the same litter size (=1) and calving interval varying from 1 to 3 years. The selected species and the values of the criteria above are in Table 3.

Table 3. Chosen model species from which survivorship curves were selected to model uncertainty in franciscana survival rates. All parameters are considered approximations as they were estimated by different methods and, in the case of maximum observed age (ω), because of intrinsic uncertainty in aging methods. AFR for most species was the age at which at least 50% of females give birth. All quantities are for females only.

Common Name	Species	Order	M (kg)	AFR	ω	T	Source
Dall's sheep	*Ovis dalli*	Artiodactyla	50	2.5	12	5.71	a
African Buffalo	*Syncerus caffer*	Artiodactyla	490	4	19	6.98	b
Zebra	*Equus burchelli*	Perrisodactyla	270	3	20	8.12	b
Northern fur seal	*Callorhinus ursinus*	Carnivora	60	3	20	10.38	c
Bottlenose dolphin	*Tursiops truncatus*	Cetacea	200	9	40	NA*	d, e

Source: a: Murie (1944) [cited in Deevey, 1947], b: Spinage (1972), c: Barlow and Boveng (1991), d: Stolen and Barlow (2003), e: Leatherwood and Reeves (1990).
*Although information on generation length (T) is not available (NA) for this population of bottlenose dolphin, it is likely between 15 and 20 years. In this case, this criterion would be satisfied. This exception was allowed only to have a cetacean among the selected model species.

To increase comparability between the model species and franciscana, the time scales of model species survivorship curves were rescaled according to franciscana's AFR, using Caswell *et al.*'s (1998) equation 2. If T_i is the time scale for model species *i*, the rescaled time for species *i* is given by:

$$\hat{T}_i = T_i \frac{AFR_{Fr}}{AFR_i}$$ [eq. 14]

where AFR_{FR} and AFR_i are the ages at first reproduction for franciscana and model species *i*, respectively. Rescaling means that, for example, a single year in the life of bottlenose dolphin (one of the model species) with AFR of about 8 to 9 years, corresponds to about half a year in the life of franciscana (with mean AFR of about 4.5 years). Caswell *et al.* (1998) took account of uncertainty in AFR estimates by rescaling using values of AFR_i randomly selected from a distribution that characterised the uncertainty in that parameter. This approach could have been used here, but we chose the

model species more carefully, most of them with AFR very close to franciscana. We also opted to use only the point estimate of the AFR. Most model species used in Caswell *et al.* had a low coefficient of variation in this estimate (less than 7% in eight of ten species and around 10% in the other two species). Incorporating uncertainty in this parameter would have resulted in little change to the resulting estimates. Since the relationship among vital rates is complex and little understood, it seems that rigour in selection of the model species is probably more important.

Rescaling could be based on maximum age (Barlow and Boveng, 1991). We decided to use AFR because data on the age distribution of franciscana are biased and therefore unsuitable for estimation of maximum age. Also, aging old individual is difficult in franciscana, complicating assessment of maximum age. This may also be the case for some of the model species. Furthermore, Krementz *et al.* (1989) have shown that observed maximum longevities derived from band recovery data for several species of North American waterfowl were not correlated with annual survival rates and appeared to be unstable over time. These authors recommended that observed maximum age not be used in life history analysis. As population growth of long-lived species is known to be most sensitive to survival of young adult females (*e.g.* Caswell *et al.,* 2001), Caswell *et al.* (1998) have suggested that scaling by AFR focuses on the most critical period of the life cycle. After rescaling, one year in the life of a model species with mean AFR at 4 years, for example, (*e.g.* zebra, buffalo, fur seal) becomes 1.125 years. The survivorship from age 0 to 1 and from 1 to 2 of franciscana is then equivalent to survivorship from age 0 to age 0.889 and from 1 to 1.778 for these model species.

In general, we can use the following equation:

$$l(x + a) = l(x)S(x)^a = l(x)\left\{\frac{l(x+1)}{l(x)}\right\}^a \qquad \text{[eq. 15]}$$

where, *l(x+α)* is the survivorship to age *x+ α* for any *α* < 1). In the examples above, *α* would be 0.889 and 0.778, respectively. To illustrate, examples of survivorship schedules of Dall's sheep and buffalo, before and after rescaling, are shown in Table 4.

Table 4. Survivorship schedules of the Dall's sheep and African buffalo before (*lx*) and after (*lx**) rescaling by the mean age at first reproduction.

Age	Resecaled	Dall's sheep	Dall's sheep	Rescaled	Buffalo	Buffalo

	age (sheep)	lx	lx*	age (buffalo)	lx	lx*
0	0	1.000	1.000	0	1.000	1.000
1	1.5	0.801	0.854	1.125	0.500	0.540
2	3	0.789	0.793	2.250	0.465	0.473
3	4.5	0.776	0.776	3.375	0.428	0.440
4	6	0.764	0.748	4.500	0.392	0.408
5	7.5	0.734	0.738	5.625	0.355	0.375
6	9	0.688	0.688	6.750	0.255	0.318
7	10.5	0.640	0.608	7.875	0.219	0.247
8	12	0.571	0.564	9.000	0.182	0.215
9	13.5	0.439	0.439	10.125	0.145	0.145
10	15	0.252	0.159	11.250	0.118	0.121
11	16.5	0.096	0.072	12.375	0.091	0.096
12	18	0.006	0.006	13.500	0.046	0.058
13	19.5	0.003		14.625	0.027	0.034
14				15.750	0.018	0.023
15				16.875	0.018	0.018
16				18.000	0.009	0.015
17				19.125	0.009	0.009
18				20.250	0.009	0.009

Age-specific survival rates of franciscana were calculated from the model survivorship schedules as follows:

1) Rescale the survivorship curve of the model species according to equation 15.

2) Select a survivorship curve (equation 13) from the set of model species using weights w generated from an (n-1)-dimensional Dirichlet distribution (Kotz *et al.*, 1997).

3) Calculate age-specific survival probabilities $S(x)$ from the selected survivorship using:

$$S(x) = \frac{l(x+1)}{l(x)} \qquad\qquad \text{[eq. 16]}$$

where $l(x)$ is the survivorship at age x.

4) Use the estimated survival rates as inputs to an age-structured Leslie matrix representing franciscana's population dynamics. From this matrix, the estimated stable age distribution (Caswell, 2001: p. 185-187), can be obtained:

5) Use the stable age distribution to calculate a weighted mean stage-specific survival rate for juveniles (non-calves immature) and adults (sexually mature) animals, as shown in equation 11.

Repeat steps 2 and 5 many times (*e.g.* 5000) to estimate the mean and standard error of the stage-specific survival rates.

Estimates of Survival

Maximum likelihood estimates of the five parameters of the Siler model are: a_1=0.1063 (SE=0.0737); a_2=0.0020 (SE=0.0051); a_3=0.0091 (SE=0.0090); b_1=0.1854 (SE=0.5864); b_3=0.3688 (SE=0.1844). The estimate of α was 0.676.

Stage-specific survival rates derived from the survivorship schedule obtained by fitting the Siler model to beachcast age-at-death data were 0.90 (SE=0.0270) for calves, 0.91 (SE=0.0235) for immature non-calves, and 0.84 (SE=0.0154) for adults. These values were calculated from the age-specific estimates shown in Figure 4. Uncertainty in the mean adult and juvenile survival rates are shown in Figure 5.

The expected age-at-death frequency from the mixture model showed very low survivorship in ages over 14 years. Because strong mortality due to senescence has not been observed in cetaceans and also due to the fact that age estimation of older individuals is difficult, especially in franciscana, the adult survival rate was estimated up to age 14. Mean adult survival rate was calculated using age classes 4 to 14, *i.e.* ignoring older individuals, given a revised estimate of adult survival of 0.854. We also restricted this estimate up to the ages of 11 because the estimates for individuals older than 10 years are very imprecise (see mortality and survival rate curves in Figure 4). The adult survival rate from age 4 to age 11 is approximately 0.88 (SE = 0.018).

Calves were underrepresented in both the bycatch and beachcast samples. This resulted in an overestimation of the calf survival rate. Because calf mortality is likely to be a combination of its intrinsic mortality and that of its mother, calf survival rate could be approximated by the square of adult survival (0.73). This means the calf is assumed to have the same survival rate as its mother and to die if the mother dies. Alternatively, a ratio between calf and non-calf survival rates observed in similar species could be used to approximate a calf survival rate for franciscana. The weighted mean of non-calf survival rate for franciscana is around 0.878. When multiplied by 0.84 (ratio between calf/non-calf survival rates of bottlenose dolphin – obtained from Wells and Scott, 1990) this results in a calf survival rate of 0.737. We chose to use the latter of these approaches because it has a clear biological interpretation.
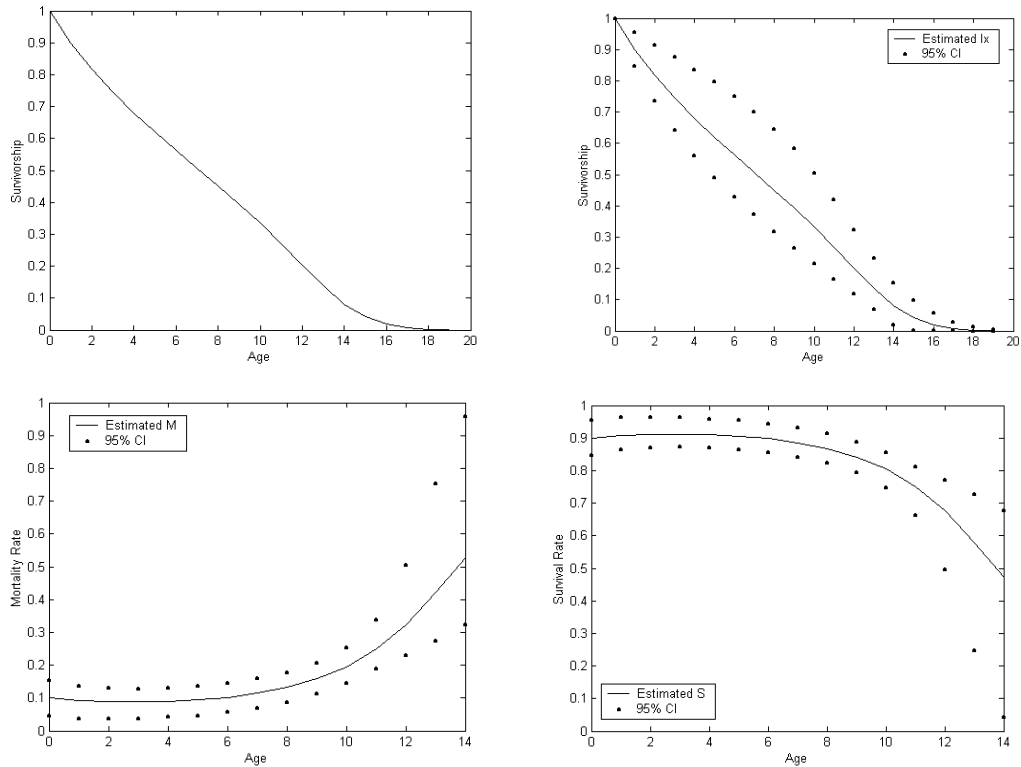
Figure 4. Mean and 95% confidence intervals of franciscana survivorship, mortality and survival rates.
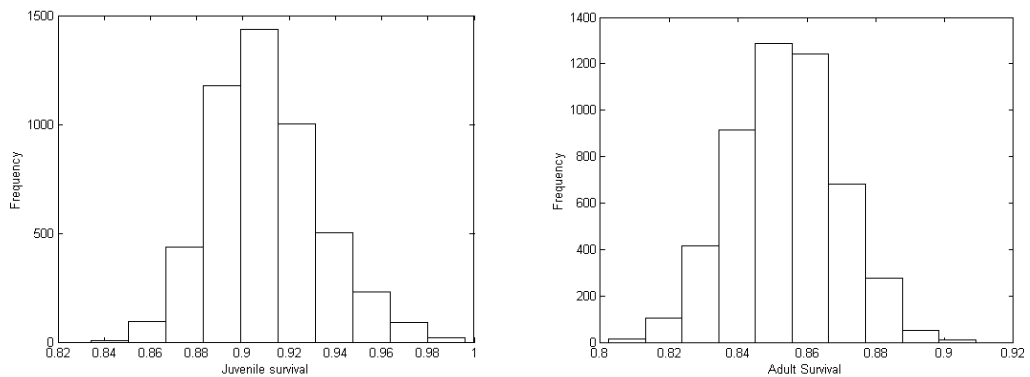

Figure 5. Frequency distribution of adult and juvenile survival rate of franciscana estimated by fitting the Siler model to beachcast age-at-death (n = 5000 runs).

Rescaled survivorship schedules and curves of the five model species are presented Table 5 and Figure 6. A Monte Carlo sample of 50 survivorship curves generated from randomly sampling the survival probabilities corresponding to the rescaled model survivorship curves fill the space where we expect the franciscana survivorship curve to be (Figure 7). The mean stage-specific survival rates estimated from the 5000 bootstrap resamples of franciscana survivorship schedules were 0.673 (SE

= 0.052), 0.883 (SE = 0.023) and 0.87 (SE = 0.016) for calves, juveniles and adult franciscanas using four model species (zebra, buffalo, northern fur seal and bottlenose dolphin) and 0.708 (SE = 0.052), 0.90 (SE = 0.022), 0.86 (SE = 0.016) when Dall's sheep is included (Figure 8). The mean stage-specific survival rates estimated by fitting the Siler model to franciscana age-at-death data of beachcast and from Monte Carlo methods using model species life tables are similar (Table 6).

Table 5. Age specific survivorship schedules (lx*) of the five model species after rescaling by the mean age at first reproduction (AFR).

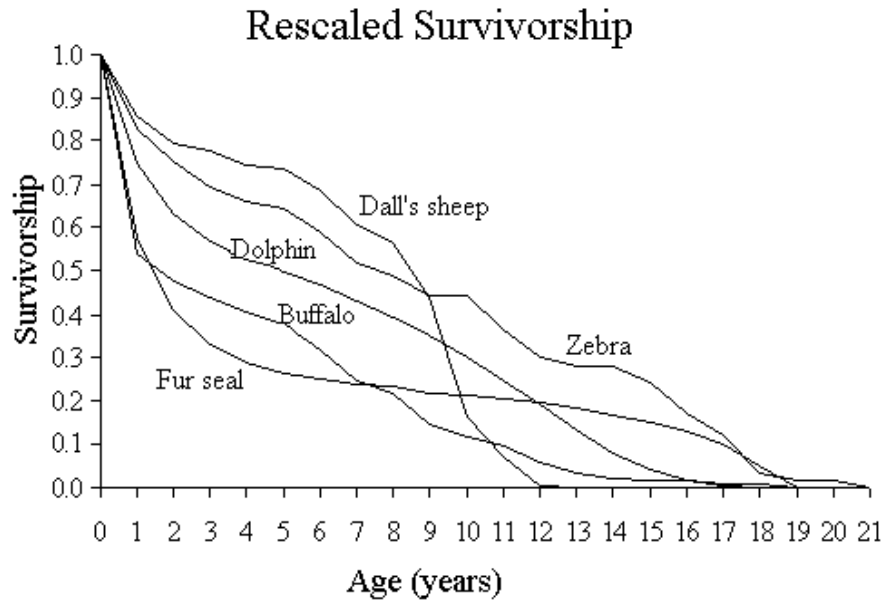| Buffalo rescaled lx*	Zebra rescaled lx*	Dolphin rescaled* lx*	Fur seal rescaled lx*	Dall's sheep rescaled lx*
1.000	1.000	1.000	1.000	1.000
0.540	0.825	0.750	0.577	0.854
0.473	0.752	0.632	0.409	0.793
0.440	0.693	0.568	0.330	0.776
0.408	0.663	0.526	0.288	0.748
0.375	0.642	0.494	0.264	0.738
0.318	0.590	0.464	0.249	0.688
0.247	0.518	0.431	0.239	0.608
0.215	0.487	0.395	0.231	0.564
0.145	0.443	0.352	0.218	0.439
0.121	0.443	0.302	0.211	0.159
0.096	0.365	0.247	0.203	0.072
0.058	0.299	0.189	0.193	0.006
0.034	0.278	0.132	0.181	
0.023	0.278	0.082	0.166	
0.018	0.241	0.044	0.148	
0.015	0.168	0.019	0.127	
0.009	0.121	0.006	0.103	
0.009	0.033	0.001	0.049	
	0.017			
	0.016			

Figure 6. Rescaled survivorship curves of the five species used as model life tables to estimate plausible range of survivorship schedules for franciscana.
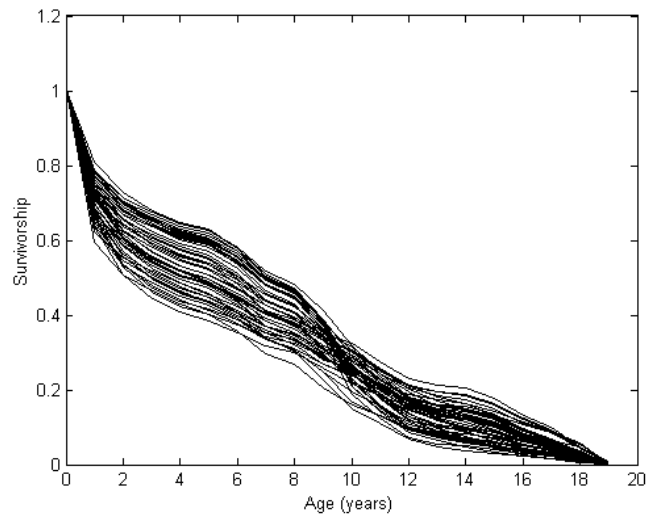

Figure 7. A Monte Carlo sample of 50 survivorship curves generated from a random sample of rescaled model survivorship curves.
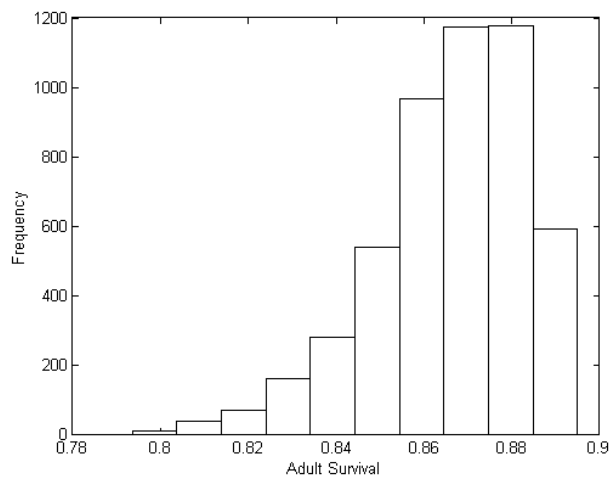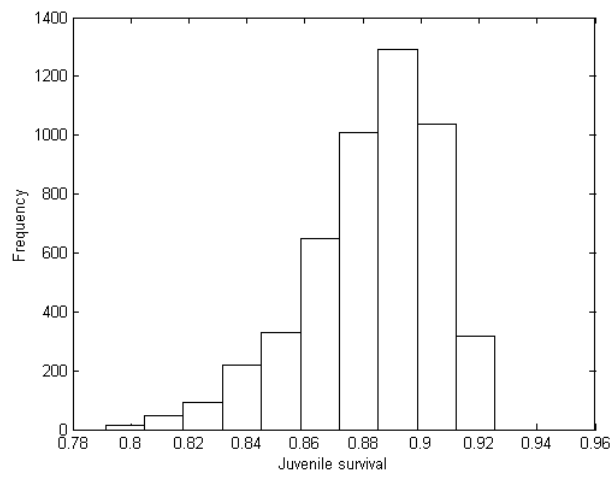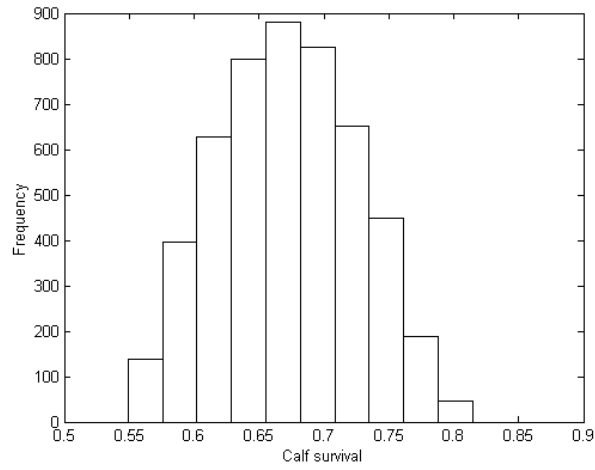
Figure 8 – Calf, juvenile and adult survival rates estimated from model species life tables of five mammal species presenting similar life histories of franciscana.

Table 6. Stage-specific survival rates mean (and SE) estimated from model life-tables of mammal species with similar life history and from franciscana species-specific age-at-death data. The later values are after adjustment for calves and adult mean survival rates.

Stage-class	Calves	Juveniles	Adults
Life-Table (w/o Dall's sheep)	0.67 (0.052)	0.88 (0.023)	0.87 (0.016)
Life-Table (with Dall's sheep)	0.71 (0.052)	0.90 (0.022)	0.86 (0.016)
Age-at-death	0.73*(a) 0.74*(b) (0.027)	0.91 (0.023)	0.854 (0.015)

*After Approximations: a - Square of Adult S
b - Ratio calf/non-calf S

Discussion

Despite their intrinsic limitations, the two methods (*i.e.* fitting the Siler model and using life tables from similar species) resulted in identical mean survival rates for juvenile franciscana. The values for adults were also identical when the age-at-death data was truncated at age 14. This suggests that bycatch age-at-death data, after careful treatment to reduce bias effects, may be useful to estimate approximate survival rates.

Life-tables from other species may be the only option to model the survivorship of many cetacean species due to a lack of data, although caution is needed when selecting the model species. This approach relies on the assumption that the chosen species have similar life histories. Relationships among life history traits are still not well understood and therefore some rigid criteria should be defined prior to the selection of model species, in order to narrow the range of species to those with very similar life histories. The decision regarding similarity of life histories is partly subjective. For example, Caswell *et al.,* (1998) used a wide range of species to represent the harbour porpoise survival schedule, including some with life histories whose similarity with harbour porpoise's is questionable. There is strong evidence for mammals (*e.g.* Millar and Zammuto, 1983; see also life traits of 50 mammal population in *Ecological Archives* E081-006) and some bird species (*e.g.* Zammuto, 1986; Krementz *et al.,* 1997) that body mass is positively correlated with survival. It seems that Caswell *et al.* (1998) overlooked this relationship and selected model species with body mass of more than one (*i.e.* killer whales, pilot whales) or even close to two (*i.e.* African elephant) orders of magnitude higher than harbour porpoise. This is likely to have the effect of pushing up the estimated survivorship of harbour porpoise. If the other model species have life histories similar to harbour porpoise (including survivorship), they will not compensate these three species (which represent 33.3% of all model species used by those authors) and the resulting estimates of survival rate will likely be overestimated. Unlike Caswell *et al.* (1998), we

used specific criteria in the selection of model species life tables, aiming to be more rigorous about the similarity between model species and franciscana life histories. We intentionally presented the survival rate estimates using life-tables with and without Dall's sheep survivorship schedule (Table 6). When Dall's sheep survivorship is included, adult survival rate is about 1% lower. This illustrates how a single species can affect the mean survival rate estimated in this way. In this case, Dall's sheep, the model species with the lowest body mass and mean age at first reproduction, brought down the mean adult survival rate. African elephant, killer and pilot whales have much higher survival rates than the species included in this study and would probably push the mean adult survival rates to values unrealistically high for franciscana.

The use of distributions of age-at-death data to estimate mortality relies on the assumption that the population has a stable age distribution. For age distribution to be stable, age-specific differences in both death rates and birth rates across age classes must be constant, and need to have been so long enough for the age structure to equilibrate. The population can depart from this ideal situation due to environmental or demographic stochasticity. In general, methods of mortality estimation are relatively robust to those types of deviation from stable conditions (Stolen and Barlow, 2003). In addition, demographic stochasticity applies to small populations only. The size of the franciscana population considered in this study is around 40,000 individuals (Secchi *et al.,* 2001). The assumption of a stable age distribution is reasonable for long-lived species: they are buffered from marked deviation from stable age structure due to their relatively long reproductive period and high survival rates (Caughley, 1966). However, high removal rates of franciscana from the population through bycatch can lead to deviations from the stable age distribution and may thereby cause bias in the mortality estimates. This problem is intensified if the age structure of the bycatch differs from the expected age distribution of the population and if age classes affected by the bycatch change through time. Therefore, estimating mortality rates or any other parameter (*e.g.* age at first reproduction) from age-at-death data which include bycaught animals has to be restricted to situations where the fishery-induced mortality process is understood to a level that allows identification of possible biases. Where possible, bias need to be removed or minimised before parameters are estimated. Beachcast data were suspected to be least biased because the animals were collected relatively close to the beginning of the expansion of gillnet fishery in southern Brazil (*ca.* 1970). The later may be important under the assumption that juveniles are more vulnerable due to the shorter learning

process about potential hazards in the environment. Moreover, at the beginning of the fishery, the age distribution of the population is expected to be similar to a stable distribution. It is well known that after a long period of fishing pressure, population structure of long-lived species will be affected, with a reduction in the proportion of old individuals (*e.g.* Pinedo, 1994). Bycatch data from Uruguay were also suspected to be minimally biased as they were collected at the beginning of the gillnet fishery expansion. In such a case, individuals from all age classes would be similarly vulnerable as there was not enough time for any learning process. The fit of the Siler model to the age-at-death data both from bycatch and beachcast (before adjustment) was poor. This is probably because franciscana age-distribution from bycatch/beachcast data is negatively biased towards calves and positively biased towards juveniles. Beachcast data also suggest strong senescent effects on the mortality pattern.

The lower vulnerability of calves to bycatch might be because they are accompanied by their mothers, which might be less vulnerable to potential hazards. It might also be because calves do not dive as deep as non-calves (gillnets in southern Brazil are set on the bottom and mostly at depths around 20m). It is also possible that calves, when caught and discarded, are less likely to be washed ashore. They may be more likely to be eaten by scavengers (*e.g.* sharks), and those that do end up washed ashore might be difficult to spot due to their small size. The strong negative bias in the number of calves in both bycatch and beachcast samples hampered the attempt to obtain mortality rates for this stage class. For these reasons, we decided to approximate the calf survival rate as the square of adult survival rate. This approach was used for harbour porpoise in Bay of Fundy, Canada and is justified on the fact that calf survival probability might be a combination of its intrinsic mortality probability and the mortality probability of its mother (Woodley and Read, 1990). Slooten *et al.* (2000) approximated the calf survival rate of Hector's for modelling purposes as a uniform distribution between the calf/non-calf survival ratio of bottlenose dolphins (ratio = 0.84) and killer whales (ratio = 0.96). We decided here to approximate calf survival rate as a ratio of calf/non-calf survival using bottlenose dolphins' value only. This is because bottlenose dolphin is the species most similar to franciscana for which appropriate data are available. Unlike Slooten *et al.,* (2000), we avoided using the ratio of calf/non-calf survival in killer whales (*i.e.* 0.96) to estimate franciscana's calf survival because of the marked difference in body mass between the two species. Calf survival is generally lower in small species as small individuals are more vulnerable to predation and to unfavourable environments.

Using the ratio for killer whales would probably overestimate calf survival for franciscanas.

Samples from wild mammal populations tend to be biased in the young age classes (Caughley, 1966). A high number of juveniles is a general pattern for most, if not all, small cetacean species incidentally caught in gillnets (see Perrin *et al.,* 1994). The reason for this pattern is not well understood, but is possibly related to the onset of a dolphin's independence from its mother. In addition, immature non-calves may have different distribution patterns from adults, they may explore the habitat more, and, they probably have less experience regarding potential hazards. A combination of factors may be the reason for this pattern. In exploited populations, the proportion of young animals is generally much higher than the expected for a population in equilibrium, as removals make the individuals less likely to reach older ages.

Although senescence plays as an important role in shaping the mortality curve of terrestrial mammals (*e.g.* Caughley, 1977; Siler, 1979), the phenomenon is not well understood and requires both evolutionary and proximate explanations (Nesse, 1988). The most widely accepted evolutionary explanation for senescence is that it is not influenced by natural selection because predation, starvation, diseases and other environmental hazards kill all wild individuals before the age at which senescence decreases fitness. The alternative explanation for the persistence of genes that cause senescence is that they have been selected for because they have pleiotropic effects that are beneficial early in the life when natural selection forces are strongest (Williams, 1957). Ness (1988) used life table data to estimate the selection pressure acting on senescence in wild populations and concluded that pleiotropic genes may be important causes of senescence in some populations but not in others. No such study exists for cetaceans. The intensity of senescence in survival may vary among phylogenetic groups and among closely related species and seems not to be strong in cetacean species for which data is available (*e.g.* killer whales - Olesiuk *et al.*, 1990; Brault and Caswell, 1993; bottlenose dolphins - Stolen and Barlow, 2003). The age-at-death data for franciscana suggest that the mortality pattern is strongly influenced by senescence. Further investigation is needed to verify whether this is real or is an artefact of the quality of the data, caused by inaccuracies in age estimation (*e.g.* Hohn and Fernandez, 1999). It is possible that some individuals older than 13 years had their ages underestimated and were placed in lower age classes (A. Hohn, pers. commn), causing an artificial pattern of senescence. We decided to restrict the data up to age 11 for estimating adult survival.

This is similar to the approach used by Caughley (1966) for Himalayan thar. The problem is a common one; sample size of older ages is generally small, resulting in very imprecise estimates. Stolen and Barlow (2003) also found high uncertainty in the mortality rate estimates for bottlenose dolphins older than 20 years. Because so few animals live up to maximum observed ages, removing the last few ages from the analysis does not affect the results to a great extent (*e.g.* Caughley, 1966). This is because relatively few individual in the older ages implies that these individuals make a smaller contribution to the weighted mean survival rate (see equation 11).

Estimated survival rates of franciscana are lower than other small cetaceans (*e.g.* Hector's and bottlenose dolphins – Cameron *et al.*, 1999; Stolen and Barlow, 2003) and much lower than medium size and large cetaceans (*e.g.* killer whales – Olesiuk *et al.*, 1990; bowhead whales - Zeh *et al.*, 1991; 1995; Givens *et al.*, 1995). This seems biologically reasonable as there is strong evidence that body mass is positively correlated with survival in mammals (*e.g.* Millar and Zammuto, 1983). Hector's dolphins however, have similar body mass to franciscanas. The explanation for the higher survival rate in Hector's dolphin is related, to some extent, to its much lower reproductive potential. A female Hector's dolphin first reproduces at approximately 8 years of age and produces one offspring every two to three years. A female franciscana, on the other hand, has its first calf at an age of approximately 4 years and reproduces every one or two years. Evolutionarily, if Hector's dolphins have limited plasticity to increase their low reproductive potential it may have been compensated by a high survival increasing the species' chance to persist. Adult survival could be influenced by density-dependent factors (Harwood and Rohani, 1996). Given the high level of incidental mortality franciscana has experienced during the last few decades, species abundance is probably far below carrying capacity. Theoretically, density-dependent factors, such as increased food availability, may have led to increased survival. However, food resources for franciscana have been depleted due to overfishing (Haimovici, 1998). Indeed changes in the diet of franciscana over time parallel the depletion of some of its main prey (Secchi *et al.*, 2003) suggesting that food availability may be a conservation issue for the species. If that is the case, adult survival could be regulated by food supply. In ungulates adult survival of large males was lower than that of females in food-limited environments (Toïgo and Gaillard, 2003). This reinforces the possibility that food availability and/or quality can affect the survival of adult franciscana.

Several dolphin species have been well-studied thanks to a large amount of biological material collected from dolphins incidentally killed in fishing operations (*e.g.* Perrin, 1975). Among other biological information about the species, samples from bycaught dolphins have been used to estimate important life-history parameters such as the age or size at first reproduction, pregnancy rate, maximum age (*e.g.* Perrin *et al.*, 1976; Kasuya, 1985; Ferrero and Walker, 1996; 1999; Iwasaki and Kasuya, 1997). Data from bycaught animals, however, are subject to biases that in some cases are difficult to quantify. For a variety of plausible reasons, which include sex/age segregation, relative abundance in the population, differences in vulnerability to entanglement in fishing gears, some age classes are underrepresented, while others are overrepresented in bycatch. There are cases where some consecutive age classes are completely absent in the bycatch sample. If these ages, for example, correspond to young mature dolphins, the age at first reproduction from these data will be underestimated (*e.g.* Iwasaki and Kasuya, 1997). Many small cetaceans have been incidentally caught in large numbers around the world. Scientists, however, have been reluctant to use data on age distribution of bycatch to estimate survival rate for those species. So far, no other study has attempted to correct bias in the age distribution of bycatch data with the purpose of using age-at-death data to estimate survival rates. The approach of this study can and should be applied to other cetacean species. However, a good understanding of the fishing related mortality process is needed. In the case of franciscana, long term dedicated studies exist to monitor bycatch and recover beachcast animals, providing large sample sizes for study.

The values obtained in this study are not meant to represent precise estimates of franciscana survival rates but only approximations for modelling purposes. These quantities can be used to model the species population dynamics as well as to make population projections useful for conservation and management.

References

Barlow, J. and Boveng, P. (1991). Modeling age-specific mortality for marine mammal populations. *Marine Mammal Science,* 7:50-65.

Birch, L.C. (1948). The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology,* 17:15-26.

Brault, S. and Caswell, H. (1993). Pod-Specific Demography of Killer Whales (*Orcinus orca*). *Ecology,* 74:1444-1454.

Bordino, P., Thompson, G. and Iñiguez, M. (1999). Ecology and behaviour of the franciscana (*Pontoporia blainvillei*) in Bahia Anegada, Argentina. *Journal of Cetacean Research and Management,* 1:213-222.

Bordino P., Siciliano, S., Bastida, R. and Cremer, M. (2002). Report of the Working Group on Distribution and Behaviour. In: Secchi, E.R. (ed.). *Biology and Conservation of Franciscana. The Latin American Journal of Aquatic Mammals,* (special issue 1):21-24.

Buckland, S.T. (1990). Estimation of survival rates from sightings of individually identifiable whales. *Reports of the International Whaling Commission,* (special issue 12):149-153.

Burgman, M.A., Ferson, S. and Akçakaya, H.R. (1993). *Risk Assessment in Conservation Biology*. (Chapman & Hall: New York.)

Calder, W.A. (1984). *Size, function, and life history*. Harvard University Press. Cambridge, MA.

Cameron, C., Baker R., Fletcher, D., Dawson, S, and Slooten, E. (1999). Modelling survival of Hector's dolphins around Banks Peninsula, New Zealand. *Journal of Agricultural, Biological and Environmental Statistics,* 4:126-135.

Caswell, H. (2001). *Matrix Population Models: Construction, Analysis and Interpretation.* 2nd Edition. Sinauer Associates, Inc. Sunderland, USA.

Caswell, W., Brault, S., Read, A.J. and Smith, T.D. (1998). Harbor porpoise and fisheries: An uncertainty analysis of incidental mortality. *Ecological Applications* 8:1226-1238.

Caughley, G. (1966). Mortality patterns in mammals. *Ecology*, 47:906-918.

Caughley, G. (1977). *Analysis of Vertebrate Population*. (Wiley: New York.)

Danilewicz, D.S. (2003). Reproduction of female franciscana (*Pontoporia blainvillei*) in Rio Grande do Sul, southern Brazil *The Latin American Journal of Aquatic Mammals,* 2:67-78.

Danilewicz, D.S., Secchi, E.R., Ott, P.H., and Moreno, I.M. (2000). Analysis of the age at sexual maturity and reproductive rates of franciscana (*Pontoporia blainvillei*) from Rio Grande do Sul, southern Brazil. *Comunicações do Museu de Ciências e Tecnologia*. PUCRS, 13:89-98.

Dawson, S.M. (1991). Incidental catch of Hector's dolphins in inshore gillnets. *Marine Mammal Science* 7(3): 283-295.

Deevey, E.S. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology* 22:283-314.

Di Beneditto, A.P.M. and Ramos, R.M.A. (2001). Biology and conservation of the franciscana (*Pontoporia blainvillei*) in the north of Rio de Janeiro State, Brazil. *Journal of Cetacean Research and Management,* 3:185-192.

Eberhardt, L.L. (1985). Assessing the dynamics of wild populations. *Journal of Wildlife Management*, 49:997-1012.

Ferrero, R.C. and Walker, W.A. (1996). Age, growth, and reproductive patterns of the Pacific white-sided dolphins ((*Lagenorhynchus obliquidens*) taken in high seas drift nets in the central North Pacific Ocean. *Canadian Journal of Zoology*, 74:1673-1687.

Ferrero, R.C. and Walker, W.A. (1999). Age, growth, and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the central North Pacific Ocean. *Marine Mammal Science*, 15**:**273-313.

Haimovici, M. (1998). Present state and perspectives for the southern Brazil shelf demersal fisheries. *Fishery Management and Ecology,* 5:277-289.

Hammond, P.S.., Mizroch, S.A. and Donovan, G.P. (Eds). (1990). *Individual recognition of cetaceans: uses of photo-identification and other techniques to estimate population parameters*. (Special Issue 12, International Whaling Commission: Cambridge.)

Harraway, J. (1993). *Introductory Statistical Methods and the Analysis of Variance*. 2nd Edition. University of Otago Press. Dunedin, New Zealand. 295pp.

Harwood, J. and Rohani, P. (1996). The population biology of marine mammals. Pages 173-190 *in* Floyd, R.B., Sheppard, A.W. and De Barro, P.J. (Eds) *Frontiers of Population Ecology*. CSIRO Publishing. Collingwood. 639pp.

Hohn, A. A. and Fernandez, S. (1999). Biases in dolphin age structure due to age estimation technique. *Marine Mammal Science,* 15:1124-1132.

Iwasaki, T. and Kasuya, T. (1997). Life history and catch bias of Pacific white-sided (*Lagenorhynchus obliquidens*) and northern right whale dolphins (*Lissodelphis borealis*) incidentally taken by the Japanese high seas squid driftnet fishery. *Reports of the International Whaling Commission,* 47:683-692.

Kasuya, T. (1985). Effects of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute,* 36**:**107-138.

Kasuya, T. and Brownell, R.L. (1979). Age determination, reproduction and growth of franciscana dolphin, *Pontoporia blainvillei. Scientific Reports of the Whales Research Institute,* 31**:** 45-67.

Kasuya, T. and Marsh, H. (1984). Life history and reproductive biology of the short-finned pilot whales, Globicephala macrorhynchus, off the Pacific coast of Japan. *Reports of the International Whaling Commission* (special issue 6):259-310.

Kotz, S., Read, C. and Banks, D.L. (eds) (1997). *Encyclopedia of Statistical Sciences*. Volume 1, Update. Wiley Europe. 582pp.

Krementz, D.G., Sauer, J.R. and Nichols, J.D. (1989). Model-based estimates of annual survival rate are preferable to observed maximum lifespan statistics for use in comparative life-history studies. *Oikos*, 56:203-208.

Krementz, D.G., Barker, R.J. and Nichols, J.D. (1997). Sources of variation in waterfowl survival rates. *The Auk*, 147:93-102.

Leatherwood, S. and Reeves, R.R. (eds) (1990). *The bottlenose dolphin.* Academic Press. San Diego. CA.

Manly, B.F.J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. 2nd Edition. Chapman & Hall (London). 399pp.

Millar, J.S. and Zammuto, R.M. (1983). Life histories of mammals: an analysis of life tables. *Ecology*, 64:631-635.

Morris, W. F., and Doak, D. F. (2003). *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, Masschusetts, USA. 480 pp.

Nesse, R.M. (1988). Life table tests of evolutionary theories of senescence. *Experimental Gerontology*, 23:445-453.

O'Corry-Crowe, G.M., Suydam, R.S., Rosenberg, A., Frost, K.J. and Dizon, A.E. (1997). Phylogeography, population structure and dispersal patterns of the beluga whale Delphinapterus leucas in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology*, 6:955-970.

Olesiuk, P.K., Bigg, M.A. and Ellis, G.M. (1990). Life history and population dynamic of resident killer whales (Orcinus orca) in the coast of British Columbia and Washington State. *Reports of the International Whaling Commission* (special issue 12):209-3.

Ohsumi, S. and Masaky, Y. (1975). Biological parameters of the Antarctic minke whale at the virginal population level. *Journal of the Fisheries Research Board of Canada*, 32:995-1004.

Ohsumi, S., Masaky, Y. and Kawamura, A. (1970). Stock of the Antarctic minke whale. *Scientific Reports of the Whales Research Institute,*22:75-126.

Perrin, W.F. (1975). Variation of the spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography of the University of California,* 21:1-206.

Perrin, W.F. and Myrick Jr., A.C. (Eds) (1980). *Age determination of toothed whales and sirenians*. (Special Issue 3, International Whaling Commission: Cambridge.)

Perrin, W.F., Coe, J.M. and Zweifel, J.R. (1976). Growth and reproduction of the spotted porpoise, Stenella attenuata, in the offshore eastern tropical Pacific. *Fishery Bulletin*, 74:229-269.

Perrin, W.F, Donovan, G.P. and Barlow, J. (Eds) (1994). *Gillnets and Cetaceans*. (Special Issue 15, International Whaling Commission: Cambridge.)

Pianka, E.R. (1978). Evolutionary Ecology. 2nd Edition. Harper & Row, New York.

Pinedo, M.C. (1991). Development and variation of the franciscana *Pontoporia blainvillei*. Ph.D. Thesis, University of California, Santa Cruz.

Pinedo, M.C. (1994). Impact of incidental fishery mortality on the age structure of *Pontoporia blainvillei* in southern Brazil and Uruguay. *Reports of the International Whaling Commission,* (special issue) 15:261-264.

Pinedo, M. C. and Hohn, A. A. (2000). Growth layer patterns in teeth from the franciscana, *Pontoporia blainvillei*: Developing a model for precision in age estimation. *Marine Mammal Science,* 16:1-27.

Press, W.H., Flannery, B.P., Teukolsky, S.A., and Vetterling, W.T. (1986). Numerical receipes: the art of scientific computing. Cambridge University Press, Cambridge, England.

Read, A. J. and Hohn, A. A. (1995). Life in the fast lane - the life-history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science* 11:423-440.

Reilly, S.B. and Barlow, J. (1986). Rates of increase in dolphin population size. *Fishery Bulletin,* 84:527-533.

Rosas, F.C.W. and Monteiro-Filho, E.L.A. (2002). Reproductive parameters of *Pontoporia blainvillei* (Cetacea, Pontoporiidae), on the coast of São Paulo and Paraná States, Brazil. *Mammalia,* 66:231-245.

Scorza-Trevino, S. and Dizon, A. E. (2000). Phylogeography, intraspecific structure and sex-biased dispersal of Dall's porpoise, *Phocoenoides dalli*, revealed by mitochondrial and microsatellite DNA analyses. *Molecular Ecology*, 9:1049–1060.

Scott, M.D., Well, R.S. and Irvine, A.B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. Page 235-244 *in* Leatherwood, S. and Reeves, R.R. (eds). *The bottlenose dolphin.* Academic Press. San Diego. CA.

Secchi, E.R. (1999). Taxa de crescimento potencial intrínseco de um estoque de franciscanas, *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844) (Cetacea, Pontoporiidae) sob o impacto da pesca costeira de emalhe. Master Thesis, Fundação Universidade Federal do Rio Grande, Rio Grande.

Secchi, E.R., Ott, P.H., Crespo, E.A., Kinas, P.G., Pedraza, S.N. and Bordino, P. (2001). A first estimate of franciscana (*Pontoporia blainvillei*) abundance off southern Brazil. *Journal of Cetacean Research and Management*, 3: 95-100.

Secchi, E.R. and J.Y.Wang (2002). Assessment of the conservation status of a franciscana (*Pontoporia blainvillei*) stock in the Franciscana Management Area III following the IUCN Red List Process. *The Latin American Journal of Aquatic Mammals,* 1 (special issue 1):183.190.

Secchi, E.R., Ott, P.H. and Danilewicz, D.S. (2003). Effects of fishing by-catch and conservation status of the franciscana dolphin, *Pontoporia blainvillei*. Pages 174-191 *in* Gales, N., Hindell, M. and Kirkwood, R. (Eds) *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing. Collingwood. 458pp.

Siler, W. (1979). A competing-risk model for animal mortality. *Ecology* 60:750-757.

Slooten, E. and Lad, F. (1991). Population biology and conservation of Hector's dolphin. *Canadian Journal of Zoology,* 69:1701-1707.

Slooten, E., D. Fletcher, and B.L. Taylor. (2000). Accounting for Uncertainty in Risk Assessment: Case Study of Hector's Dolphin Mortality due to Gillnet Entanglement. *Conservation Biology,* 14: 1264-1270.

Spinage, C.A. (1972). African ungulate life tables. *Ecology*. 53:645-652.

Stearns, S.C. (1976). Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, 51:3-47.

Stearns, S.C. (1983). Influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 41:173-187.

Stolen, M. K. and Barlow, J. (2003). A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon System, Florida, USA. *Marine Mammal Science* 19(4): 630-649.

Toïgo, C. and Gaillard, J.-M. (2003). Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos*, 101:376-384.

Tønnessen, J.N. and Johnsen, A.O. (1982). *The history of modern whaling*. Australian National University Press. Canberra.

Wade, P. (1998). Calculating limits to allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, 14:1-37.

Wells, R.S. and Scott, M.D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Reports of the International Whaling Commission,* (special issue) 12: 407-415.

Western, D. and Ssemakula, J. (1982). Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia*, 54:281-290.

Williams, G.C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution*, 11:391-411.

White, G.C. and Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study,* 46 (Supplement):120-138.

Woodley, T.H. and Read, A.J. (1991). Potential rate of increase of a harbour porpoise (*Phocoena phocoena*) population subject to incidental mortality in commercial fisheries. *Canadian Journal of Fisheries and Aquatic Science,* 48:2429-2435.

Zammuto, R.M. (1986). Life histories of birds: clutch size, longevity, and body mass among North American game birds. *Canadian Journal of Zoology*, 64:2739-2749.

Zeh, J.E., George, J.C., Raftery, A.E. and Carroll, G.M. (1991). Rate of increase, 1978-1988, of bowhead whales, *Balaena mysticetus*, estimated from ice-based census data. *Marine Mammal Science*, 7:105-122.

Zeh, J.E., George, J.C. and Suydam, R. (1995). Population size and rate of increase, 1978-1993, of bowhead whales, *Balaena mysticetus*. *Reports of the International Whaling Commission*, 45:339-344.