Life-history tables of the Mediterranean fin whale from stranding data

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ORIGINAL ARTICLE

Life-history tables of the Mediterranean fin whale from stranding data

Massimo Arrigoni[1,2], Piero Manfredi[3], Simone Panigada[2], Lorenzo Bramanti[1,4] & Giovanni Santangelo[1]

1 Department of Biology, University of Pisa, Pisa, Italy
2 Tethys Research Institute, Milan, Italy
3 Department of Statistics and Mathematics Applied to Economics, University of Pisa, Pisa, Italy
4 Institut de Ciencias del Mar, CSIC, Barcelona, Spain

Abstract

The conservation of long-lived species requires extensive, in-depth knowledge of their population structure and vital rates. In this paper we examine the structure of the Mediterranean fin whale (*Balaenoptera physalus*) population based on the available mortality figures from European stranding network databases compiled over the past 22 years. Such data has enabled us to lay out a first life-history (mortality) table of the population using a simple age-structured demographic model with three life-tables: calf, immature and mature. Our results reveal a high mortality rate in the first stage of life (77% per year), which decreases during the immature stage and falls further during the mature adult stage. In addition, we have calculated the corresponding life expectancies at birth (e_0), at entry in the immature stage (e_1) and at maturity (e_2) under different hypotheses on survival at the maximum age of 90 years (s_{90}) ranging between 0.1 and 3% of newborns still alive. The life expectancy at birth (e_0) at the lower bound of the chosen range ($s_{90} = 0.001$) is about 6 years, entry in the immature stage (e_1) is 8.2 years, and entry in the mature stage (e_2) is about 15.6 years. This large increase is the consequence of the higher mortality in the first two stages compared with the mature one. The life expectancies are 10.1, 14.3, and 37.8 years for s_{90} at the upper bound of the chosen range ($s_{90} = 0.03$). The resulting population intrinsic growth rates (r) ranged between -1.3 and $+1.7$ per year. High juvenile mortality patterns imply that the stationary reproductive value (the number of female offspring produced by each female after a given age x) at the start of maturity reaches a value about seven times higher than at birth. Only optimistically high survival patterns of older individuals would allow positive intrinsic growth rates, thereby enhancing the chances of the population survival.

Introduction

Surprisingly, the fin whale (*Balaenoptera physalus*), which is the world's second largest cetacean and one of its longest-lived mammals (Lockyer *et al.* 1977), is also one of the least-known Mysticetes in demographic terms (Notarbartolo di Sciara *et al.* 2003).

While some demographic studies have been conducted using industrial whaling data on Northeast Atlantic populations (Aguilar & Lockyer 1987), little is known about the demography of their counterparts in the Mediterranean, where industrial whaling has never been practised (Notarbartolo di Sciara *et al.* 2003). Although the data from Aguilar & Lockyer (1987) are a fundamental

contribution to the understanding of the demography of the fin whale, no population dynamics model has ever been developed for this species. Moreover, as the Mediterranean fin whale population is genetically distinct from its Northeast Atlantic counterpart (the nearest population in geographic terms; Bérubé *et al.* 1998; Palsboll *et al.* 2004), it therefore represents a separate unit of conservation, requiring *ad hoc* studies.

According to the IUCN *Red data book* criteria (Reeves and Notarbartolo di Sciara, 2006), the conservation status of this Mediterranean species has been judged *data deficient* due to the lack of demographic information. However, a more recent assessment, still under review by the Red List Authority, has classified the Mediterranean population as vulnerable (Panigada, pers. comm.)

The survival of this population is threatened by many sources of mortality and environmental stress (Notarbartolo di Sciara & Gordon 1997; Notarbartolo di Sciara *et al.* 2002), the most important of which are ship collisions (Panigada *et al.*, 2006), fishing gear entanglement, human-induced natural habitat degradation, unregulated whale-watching (Airoldi *et al.* 1999), and acoustic disturbance (Notarbartolo di Sciara *et al.* 2003; Abdulla *et al.* 2008). Although some ecological features, such as seasonal abundance (Forcada *et al.* 1996), habitat use (Panigada *et al.* 2005, Panigada *et al.* 2008; Monestiez *et al.* 2006; Laran & Gannier 2008), site fidelity, diving profiles (Panigada *et al.* 1999) and contamination by pollution (Fossi *et al.* 2003) have been investigated, no population dynamics study has been performed on fin whale populations to date.

Only recently have the demographic models widely used in studying other animal and plant populations (Ebert 1998; Caswell 2001; Santangelo & Bramanti 2006) been applied to the study of cetaceans (Buckland 1990; Fujiwara & Caswell 2001). Two different approaches are commonly applied in demographic studies; these are based on *static* or *cohort life-tables*. A third approach is to compile *mortality tables* (Caughley 1966; Caughley & Sinclair 1994; Ebert 1999), which provide precise information about size/age and sex of dead individuals. Herein we have adopted this latter approach, which to date has never been applied to cetaceans, by using stranding data. Our aim is to develop a demographic model for the Mediterranean fin whale population based on a life-history table (mortality table *sensu* Bergher 1990; Ricklefs and Miller 2001) built on Mediterranean stranding records.

Material and methods

Stranding data

Our demographic model has been based on all available data on fin whale strandings recorded on Mediterranean coasts between 1986 and 2007. The information on strandings along the Italian coasts has been drawn from the CSC (Cetacean Study Center) database, available online at CIBRA (2010). The Spanish and French coast stranding data have been collected respectively from the MEDACES database (2009) and the French National Stranding Network RNE (2008). Further data from Mediterranean countries without dedicated stranding databases were found in the scientific literature (Notarbartolo di Sciara *et al.* 2003). In our analyses we used the stranded animals' sex and length at death. Unfortunately, the information is not uniform, as in many cases sex was not determined and exact size measurements are possible only for recently dead animals due to their rapid decomposition.

Basic life-history data

Fin whales are characterized by fast growth in the first part of their life, which then slows as they reach full physical maturity at about 25 years of age (Aguilar & Lockyer 1987). As a first step, we transformed the size distribution of the stranded whales into a size-stage distribution, and then into an age distribution by stage. This was carried out using the growth and reproductive parameters measured in the Northeast Atlantic population (Lockyer 1984; Aguilar & Lockyer 1987; Aguilar *et al.* 1988), criteria which yielded the following three age-stages: Calf (0–0.5) years, Immature (0.5–7.5) years, and Mature (7.5–90) years. The value of 90 years represents the maximum life-span for fin whales estimated by Lockyer *et al.* (1977).

As a preliminary assumption we hypothesized that stranding data represent a faithful description of the real mortality by stage. This, however, holds only if the probability of stranding is equal in all life-tables. Indeed, only under such circumstances would we expect the relative distribution of stranding by stage to be the same as the true underlying distribution of deaths by stage. As precise information in this regard is lacking, such an assumption is therefore necessary to compute the mortality table.

The mortality table

To build up a complete mortality table for the population we used a simple demographic model based on the three above-defined life-tables, with continuous age distribution and constant mortality rates within each stage, under the assumption of population stationarity (*i.e.* the population is assumed to be constant in number and age structure over time).

As we assumed that no animals survive beyond the age of 90, to apply the model with constant mortality rates, it is necessary to know the fraction (s_{90}) of newborn individuals that survive up to the maximum age $\omega = 90$.

Given the lack of information on this quantity, we performed a detailed analysis of the sensitivity of the life-table to different assumptions on survival rates up to the maximum age (ranging between 0.1 and 3%). This has enabled us to compute the mortality rates (or mortality risks) μ for each age-stage (a_{i-1}, a_i) via the equation:

$$\mu_i = \left(\frac{-1}{a_i - a_{i-1}}\right) \log\left(\frac{s(a_i)}{s(a_{i-1})}\right) \qquad (1)$$

In equation 1, the age interval (a_{i-1}, a_i) denotes the i-th age-stage. Thus, as per the definitions in the previous section, the calf stage is defined by $(a_0 = 0, a_1 = 0.5$ years), the immature stage by $(a_1 = 0.5$ years, $a_2 = 7.5$ years), and the difference $h_i = a_i - a_{i-1}$ is the corresponding class length. Finally, $s(a_i)$ denotes the fraction of newborn individuals still alive at precisely age a_i [*i.e.* at the moment of transition from stage i to stage $(i + 1)$].

The assumption of constant mortality rates within each age group implies that the corresponding survival curve has the following exponential form:

$$s(a) = s(a_{i-1})e^{-\mu_i(a-a_{i-1})} \qquad a_{i-1} \leq a < a_i \qquad (2)$$

Equation 2 means that the fraction(s) surviving at any given age a in each age group can be computed from the fraction surviving at the age of entry into the group and reducing this fraction by the mortality risk μ_i, which 'accumulates' as the individual grows older. It is worthwhile noting that equation 1 is easily derived by setting $a = a_i$ in equation 2 and solving for μ_i.

In addition, we have calculated other standard life-table statistics, such as the life expectancy at birth (e_0) and the life expectancies upon entry into subsequent stages (e_i). The life expectancy at birth, which is easily computed as the area below the survival curve (2), represents the number of years that a newborn individual is expected to live if exposed during its lifetime to the mortality risks described by the mortality table (Keyfitz & Caswell 2007). A similar interpretation is attributed to the life expectancy at the moment of entry into the mature stage e_2: this represents the number of years that an individual just entering the mature stage is expected to live if exposed during the rest of its life to the mortality risks described by the mortality table. Such measures provide a useful summary view of mortality.

Reproduction parameters

The fertility rates for females have been drawn from the literature using the standard assumption that a mature female that has not been subjected to mortality produces on average one offspring every 22–24 months (Lockyer 1984). This corresponds to an age-specific female fertility rate of about 0.25–0.28 females per year, assuming a sex ratio at birth of 1:1 (Zanardelli *et al.* 1999). By combining this assumption with our mortality table, we have calculated the standard reproduction measures: the net reproductive number (R_0), the mean age of mothers at reproduction in the corresponding stationary population (T), the population intrinsic growth rate (r, Keyfitz & Caswell 2007) and the reproductive value at each age in a stationary population (SRV). The net reproductive rate R_0 represents the average number of female offspring a female expects to have during her entire life under the mortality described by the given life-table (so that the value $R_0 = 1$ represents the threshold between population growth and decline). The stationary reproductive value (SRV) represents the number of female offspring remaining to be born to a female mother after any given age x. Further details are reported in Appendix 1.

Results

Stranded population structure

The final dataset includes 134 individuals of known size, but whose sex was identified only in 73 cases (33 males and 40 females). The hypothesis of a balanced sex ratio in the subsample of known sex was not rejected (Chi-squared test, $\chi^2 = 0.0833$ NS). However, given the small figures for each gender, we decided to compute a unique mortality table for the two sexes.

The time distribution of total strandings (Fig. 1) does not suggest any evident trend. Figure 2 reports the distribution of strandings by life-table in two distinct 11-year subperiods: 1986–96 and 1997–2007 and throughout the
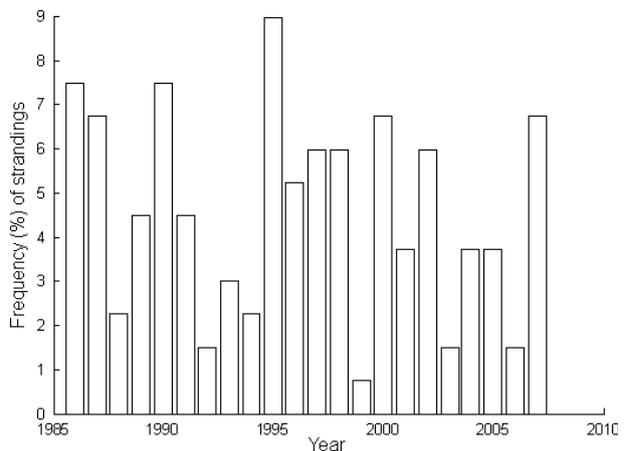
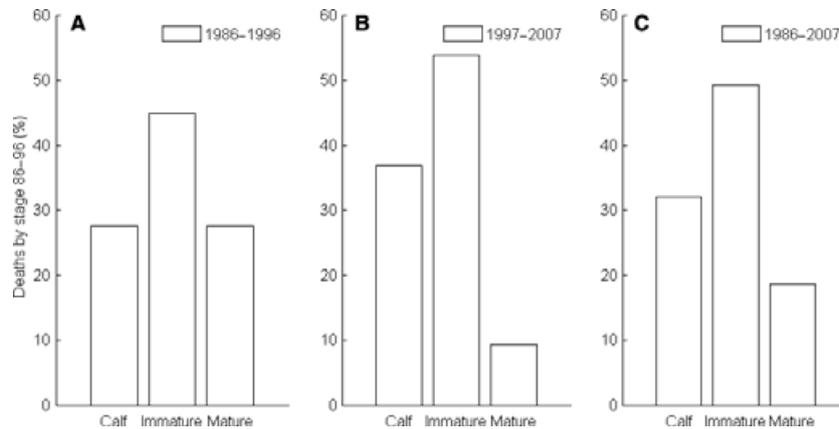**Fig. 1.** Mediterranean fin whale: distribution of total strandings over the period 1986–2007.

Fig. 2. Mediterranean fin whale: distribution of strandings by life-stage over two different periods: (A) 1986–96, (B) 1997–2007, and (C) the entire measurement period: 1986–2007.

entire period. There was a statistically significant difference in the population mortality structure between the two 11-year periods (omnibus-type likelihood ratio test on the multinomial distribution significant at 1%), suggesting that some change in mortality could have occurred in the more recent period (1997–2007). However, even though the data suggest the possibility of a change in the mortality structure, we calculated a single mortality table for the entire period to avoid the excessively small sample size that would result by splitting the data. This was supported by the lack of any evident trends in the distribution of total strandings over time (Fig. 1), as well as by some evidence of stability suggested by the monotonically decreasing structure of the normalized data (Table 1, Fig. 3).

Mortality table

As a second step we built a new mortality table (Table 1) based on the strandings according to occurrence in the three discrete life-tables into which the species life cycle has been divided (calf, immature and mature). In this perspective, the total number of strandings (134) can be interpreted as the number of newborns in a hypothetical birth cohort, of which 43 die during the calf stage, 66 during the immature stage, and the remaining 25 individuals during the mature stage (Table 1 column 5). Interpreting the data is simplified by using a hypothetical

cohort of 1000 (instead of 134) recruits, as shown in Table 2, column 3: of 1000 recruits, only 679 (67.9%) enter the immature stage and only 186 enter the mature stage. Under the stationarity hypothesis, this represents the living population structure.

Clearly, the distribution of individuals by life-tables is biased by the different durations of the stages. To correct for this, we normalized the distribution to the duration of the first stage (6 months), which is the shortest (Table 1).

Using equation 1, we computed the continuous mortality rates μ_i inside each stage. For calves, μ_1 was 0.774 per year, while for immature individuals, μ_2 was 0.184 per year, less than a quarter of the calf rate. For mature whales the mortality rate ranged between 0.063 per year for $P_{90} = 0.001$ and 0.022 per year for $P_{90} = 0.03$.

Figure 3 shows the corresponding survival curves computed according to equation 2 using the values $P_{90} = 0.001$ and $P_{90} = 0.03$. The plotted survival curves differ from each other only in the third age-stage (7.5–90 years), a consequence of the different assumptions on the fraction surviving at 90 years. The curves furthermore show first an exponentially decreasing pattern within each age-stage, a result of the assumption of constant-rate mortality in each stage, and secondly a marked difference in the rate of decline in the different stages, which is consistent with the different mortality rates in the various stages.

Table 1. Mediterranean fin whale: mortality table by life-stages.

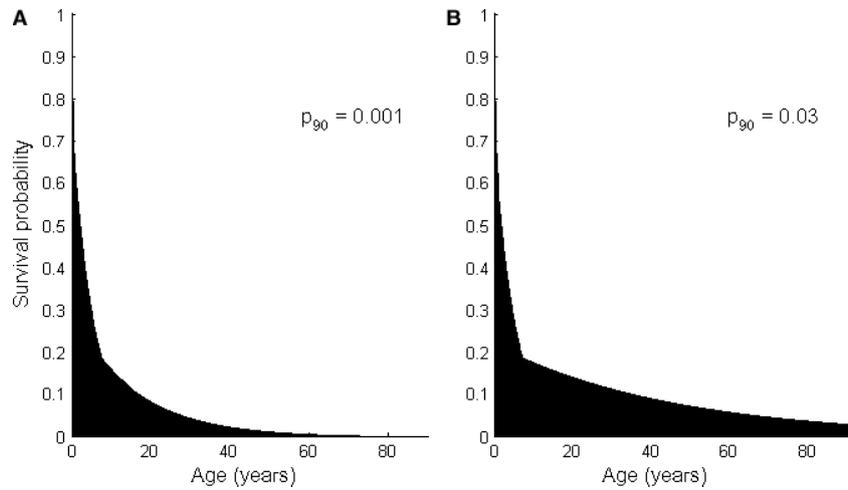| Life-table	No. of deaths	Stage duration (years)	No. of deaths normalized by stage duration (year^{-1})	No. of survivors at onset of each stage	No. of survivors at onset of each stage (per 1000)
Calf	43	0.5	86	134	1000
Immature	66	7.0	9.42	91	679
Mature	25	82.5	0.30	25	186

Fig. 3. Mediterranean fin whale: age-specific survival curves under two different assumptions on the probability of survival to maximum age: (A): $p_{90} = 0.001$; (B) $p_{90} = 0.03$.

The life expectancies at the age of onset of the various stages (Fig. 4) show a marked increasing trend as a function of both the age of entry and the fraction surviving at age 90. In particular, for s_{90} at the lower bound of the chosen range ($s_{90} = 0.001$), the life expectancy at birth (e_0) is about 6 years, whereas the life expectancy upon onset of the immature stage (e_1) is 8.2 years, and the life expectancy entering into the mature stage (e_2) is about 15.6 years. This large increase follows from the very high mortality in the first two stages as compared with the mature stage.

At the upper bound of the chosen range ($s_{90} = 0.03$) the respective life expectancies are 10.1, 14.3, and 37.8 years.
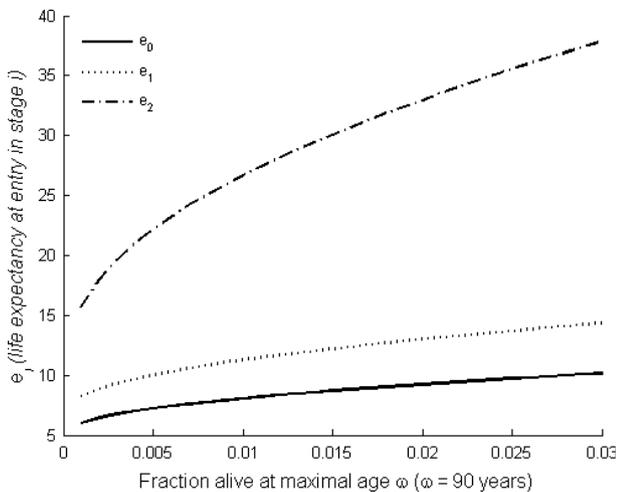
Reproduction parameters

By combining our set of mortality tables with fertility data we can develop scenarios of long-term population trends. The net reproductive rate R_0 ranges from a value well below one (0.73) for the $s_{90} = 0.001$ hypothesis, to a value considerably above unity (1.77) for $s_{90} = 0.03$. The mean age of mothers at reproduction correspondingly ranges between 22.8 and 36.8 years (Fig. 5). Finally, the corresponding intrinsic population growth rate (r) ranges between -1.3% and $+1.7\%$ year^{-1} (Fig. 6). Figure 7 shows the trend of the SRV with the age of the mother. In particular, the value at sexual maturity is about seven times higher than the value at birth, due to the huge mortality during pre-reproductive ages.
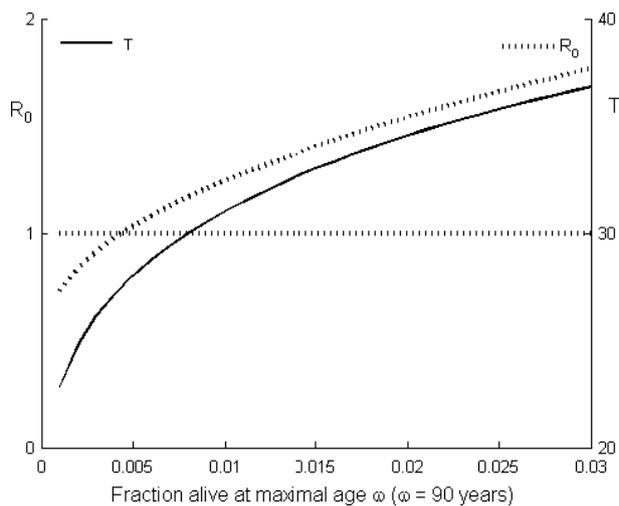

Fig. 4. Mediterranean fin whale: life expectancies at the age of entry into the various stages as functions of the fraction surviving at age 90 (ranging between 0.001 and 0.03); e_0 = life expectancy at birth, e_1 = life expectancy at onset of the immature stage, e_2 = life expectancy at onset of maturity.

Fig. 5. Mediterranean fin whale: net reproduction rate R_0 (left vertical axis) and the corresponding mean age of mothers at reproduction T (right vertical axis) as functions of the fraction surviving at age 90.
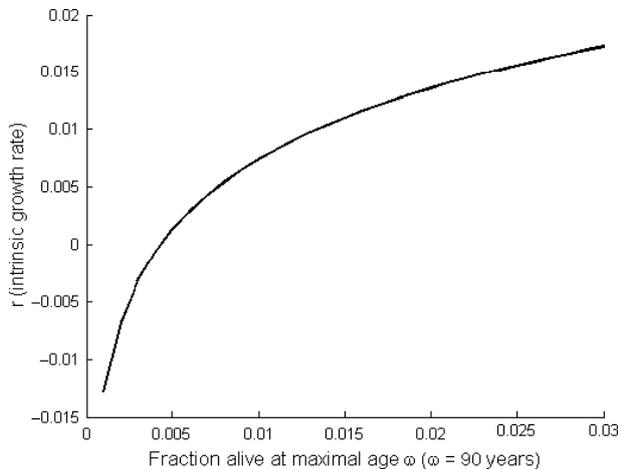
Fig. 6. Mediterranean fin whale: the population intrinsic growth rate as a function of the fraction surviving at age 90.
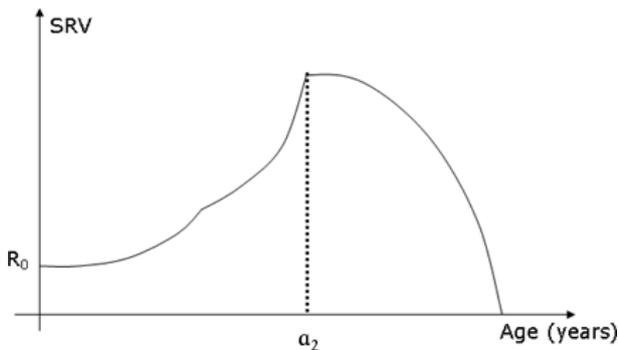

Fig. 7. Mediterranean fin whale: change in the stationary reproductive value (SRV) with age; a_2 is the age at sexual maturity.

Discussion

This study seeks to describe the structure of the Mediterranean fin whale population by analyzing stranding records from the period 1986–2007. As the ecological characteristics of this species make data collection at sea particularly difficult (fin whales usually live far from the coast and are difficult to observe due to weather constraints and the high costs of dedicated research vessels), strandings may prove to be an alternative source of demographic data (Orsi Relini *et al.* 2004). This study is the first to analyze the demographic features of the Mediterranean fin whale population and, to our knowledge, the first to set out a mortality table based on cetacean stranding data.

The dataset examined does not reveal any significant divergence from a balanced sex ratio in the strandings. We are therefore unable to confirm the natural bias towards female mortality previously suggested for this species (Clark 1982; De La Mare 1985).

Our results show that the first stage of the life cycle is the most life-threatening, with a yearly risk of death of about 77%, whereas in the immature stage, death is nearly four times less likely (18%). This indicates a strong impact, natural and/or anthropogenic, on calves and immature animals, which prevents their reaching sexual maturity. On the other hand, the risk of death of mature individuals is much lower: under the most pessimistic scenario it is still only about 6.3% per year. These results confirm a pattern common to several mammals: high mortality in the youngest age classes and low ones in mature stages (Caughley 1966; Emelen 1970). Nonetheless, a very low proportion of newborns reach sexual maturity, which may represent a serious threat for the survival of this population. Indeed, even under very optimistic hypotheses on the length of the maximum lifespan and prolonged fertility, the intrinsic growth rate r is likely to be positive only if the percentage of offspring surviving up to maximum age is quite high (*i.e.* well above 0.005). The SRV clearly shows that the contribution to the population in terms of survival is biased toward adults: most calves and young whales do not contribute to reproduction because they will never reach sexual maturity.

In conducting this study we examined all the available data on strandings. However, these are far from representative of all Mediterranean strandings. In addition, only some of the available data were suitable for analysis, as indications on sex are lacking in about half the cases and the reported size is often approximate or even missing. To make up for this lack of data uniformity, we resorted to some necessary assumptions (population stationarity and identical stranding probabilities in each stage). Although the proposed model is rather simple, the study nevertheless suggests that stranding data and the use of demographic models may well allow enhancing our currently limited knowledge of the demographics of this important cetacean. Future work to improve our ongoing study of fin whale populations will focus on comparing the approach applied herein with analyses of photo-identification data recorded by the Tethys Research Institute on the live population inhabiting the waters of the Pelagos Sanctuary. We also plan to investigate population dynamics under different conservation scenarios, and thereby assess its current status and risk of extinction.

At present, in spite of the existence of the Pelagos Sanctuary (Notarbartolo di Sciara *et al.* 2007), an MPA specifically designated to protect cetaceans and which represents the most important feeding grounds for the Mediterranean fin whale (Notarbartolo di Sciara *et al.* 2003), no specific regulation is currently in force for protection of this species. Regulation of naval traffic and

whale-watching activities could enhance this population's chances of survival (Panigada *et al.*, 2006).

Our findings suggest that mitigation measures targeted to reproductive adults, particularly addressed to increase the mean age of mothers at reproduction, are likely to be the most effective and need to be taken into account in designing proper conservation plans. The discovery of breeding grounds where calves may enjoy greater protection, could further increase survival rates. On another track, special naval traffic regulations, aimed at reducing mortality rates from ship collisions, could enhance the survival of mature females and calves. Mitigating other sources of mortality and stress, such as chemical and acoustic pollution, whale-watching activities and natural habitat degradation, could further improve the population's chances of survival.

Acknowledgements

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Appendix

We report some technical details on the various demographic measures used in the paper.

The mathematical model of the mortality table

The mortality table is based on the following piecewise constant mortality rate over the various (continuous) age-stages $[a_{i-1}, a_i)$

$$\mu(a) = \begin{cases} \mu_i & a_{i-1} \leq a < a_i \\ \infty & a \geq a_n = \omega \end{cases} \qquad (A1)$$

In particular, all individuals alive at the maximal age $a_n = \omega$ are assumed to suddenly die, which amounts to assuming a mortality rate equal to infinity. In the simplified model described in the paper there are only three age-stages $(a_0, a_1), (a_1, a_2), (a_2, a_3 = \omega)$ representing the calf, the immature, and the mature stages.

The corresponding survival function, which represents the probability that a newborn individual dies after age a (and therefore 'survives' at least until age a) and relates to the mortality rate by the general relation $s(a) = \exp\left[-\int_0^a \mu(a)da\right]$, is given in our model by

$$s(a) = \begin{cases} s(a_{i-1})e^{-\mu_i(a-a_{i-1})} & a_{i-1} \leq a < a_i \\ 0 & a \geq a_n \end{cases} \qquad (A2)$$

which defines a piecewise exponential survival function over each age-stage.

Let $h_i = a_i - a_{i-1}$ denote the size of the i-th age-stage. The life expectancy at birth, *i.e.* the life expectancy at entry in the stage of calf, is given by:

$$e_0 = \int_0^{a_n} s(a)da = \sum_{i=1}^{n} \left(\sum_{j=1}^{i-1} e^{-\mu_j h_j} \right) \frac{1}{\mu_i} \left(1 - e^{-\mu_i h_i} \right) \quad (A3)$$

Similar equations can be derived for the life expectancies at the age of entry in the immature and mature stages, denoted by e_1, e_2 in the main text. For example the life expectancy at the age a_2 of entry in the mature stage is given by:

$$e_2 = \int_{a_2}^{a_3=\omega} \frac{s(a)}{s(a_2)} da = \frac{1}{\mu_3} \left(1 - e^{-\mu_3(\omega-a_2)} \right) \quad (A4)$$

By combining the life-table with suitable assumptions on age-specific fertility rates of female whales (taken as given) we can compute a variety of reproduction indices. Following the assumption adopted in the text, the age-specific fertility rate is given by:

$$m_F(a) = \begin{cases} m_F & a_2 < a < a_3 \\ 0 & \text{elsewhere} \end{cases} \quad (A5)$$

i.e. it is unchanging over time and constant over the whole mature stage.

Therefore, it quickly follows that:

$$R_0 = m_F s_2 e_2 \quad (A6)$$

i.e. that the Net Reproduction Number R_0 factorises as the product of the fertility rates times the probability of surviving until the mature stage times the life expectancy in the mature stage. The corresponding mean age of mothers at the birth of their female offspring (computed with reference to the stationary population of birth density $R_0^{-1} m(a)p(a)$) is given by;

$$T = \left(a_2 + \frac{1}{\mu_3} \right) - (\omega - a_2) \frac{e^{-\mu_3(\omega-a_2)}}{1 - e^{-\mu_3(\omega-a_2)}} \quad (A7)$$

The intrinsic growth rate r of the population, which represents the speed of growth or decay that the population would achieve in the long-term on the assumption that the vital rates are maintained constant over time, is given as:

$$r = m_F p(a_2) e^{-ra_2} \left(1 - e^{-(r+\mu_3)(\omega-a_2)} \right) - \mu_3 \quad (A8) m10$$

In the paper we also computed a quantity that we called the Stationary Reproductive Value (SRV), which represents, on the assumption that the population is stationary, the number of female calves remaining to be born to a female after any given age a. This function is defined as:

$$SRV = \int_a^{\omega} \frac{s(x)}{s(a)} m_F(x)dx$$