Title: Epizootic effect and aftermath in a pilot whale population

Authors: Philippe Verborgh^{1*}, Pauline Gauffier¹, Clémentine Brévar¹, Joan Giménez^{1,2}, Ruth Esteban¹, Morgane Carbou¹, Elodie Debons¹, Renaud de Stephanis¹

1. CIRCE, Conservation, Information and Research on Cetaceans. 11390 Pelayo-Algeciras, Cadiz, Spain

2. Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain

***Corresponding author:** philippeverborgh@gmail.com

Abstract

1. Over the last three decades emerging infectious diseases have produced large mortalities in wild populations.
2. Different strains of Morbillivirus have infected cetaceans all over the world and caused at least seven epizootics since the 1980s but few data exist on their effect at the population level.
3. The demographic effect of a morbillivirus epizootic was studied on a well monitored resident population of long-finned pilot whales in the Strait of Gibraltar.
4. Results show decreases in population size and apparent survival rate, especially in males, as well as negative population growth rates during the epizootic and the following years.
5. Although different anthropogenic and natural factors may have acted in conjunction, the epizootic was most likely the cause of this observed decline.
6. This epizootic and potential future ones may put the population's future at even greater risk, while their habitat is threatened by increasing anthropogenic stress.

Key words: Ocean, disease, monitoring, mammals, pollution, modelling

Introduction

Diseases outbreaks have been at the centre of attention not only when they affect humans but also wildlife (Daszak, Cunningham, & Hyatt, 2000). Their effects can even cause the extinction of small populations, (e.g., Burrows, Hofer, & East (1994)) and should therefore be monitored. A well studied example is the population of northern Europe's harbor seals (*Phoca vitulina*) that have gone through 2 phocine distemper virus epizootics causing between 50-60% mortality in a population numbering in the tens of thousands individuals (Bodewes et al., 2013; Rijks et al., 2005). On both occasions the population recovered rapidly to numbers observed before the epizootic in around 8 years. Cetaceans are no exceptions with 24 species infected by one of the six different strains of cetacean morbillivirus (CeMV) identified worldwide (Van Bressem, Duignan, & Banyard, 2014). However, only seven CeMV epizootics have been registered from stranding data since the early 1980s, affecting bottlenose dolphins (*Tursiops truncatus*), striped dolphins (*Stenella coeruleoalba*) and long-finned pilot whales (*Globicephala melas*) (Van Bressem et al., 2014). Nevertheless, the demographic effect on live populations is rarely known (Van Bressem et al., 2014). Over the winter 2006-07 the stranding rate of long-finned pilot whales along the Strait of Gibraltar coast increased 10 fold and was linked to a CeMV epizootic which spread eastward in the Mediterranean Sea during the following months (Fernández et al., 2008). The Strait of Gibraltar population had a high survival rate and a positive annual population growth rate before the epizootic (Verborgh et al., 2009). In the nearby Alboran Sea, the survival rate of some pilot whales social clusters decreased by 37.2% after the epizootic event (Wierucka et al., 2014).

As top marine predators living in offshore waters, pilot whales provide information about the state of their environment. The understanding of their population dynamic is therefore crucial to inform the administration. Indeed, monitoring of long-finned pilot whales in southern Spain has been included as an indicator of good environmental status within the Spanish implementation of the European Marine Strategy Framework Directive (2008/56/EC).

This study assessed for the first time the effect of a morbillivirus epizootic on the population size, annual survival rate and population growth rate of free-ranging long-finned pilot whales up to five years after the epizootic.

Methods

Data collection

The study area is the Strait of Gibraltar located between 5°W and 6°W. Survey transects were conducted randomly but were carried out to cover the whole range of bathymetry of the Strait for each secondary sessions from May to September. The photo-identification protocol followed Verborgh et al. (2009). Under this protocol, the researchers took pictures of completely exposed left side dorsal fins of all pilot whales surfacing in the vicinity of the research vessel. Pilot whales are swimming most of the time against the predominant easterly current. Therefore, the left side is facing south where it is best lit by the sun. All the individuals in a sighting were photographed, irrespective of their level of marking in order to have the same capture probability for all individuals. Between 1999 and 2003 all pictures taken were developed as slides, then since 2004 they were taken from a digital camera. Each photograph was analysed and data about fin image quality (from Q0 worst to Q2 best) and individual identification

codes were entered in a database.

The dorsal fin close-ups allowed marked individuals to be identified based on the natural features or marks of the dorsal fins (shape, notches and nicks) (Ottensmeyer & Whitehead, 2003). Matches with previously identified individuals were made by comparing each new photograph with all the others in the catalogue. Marked animals that could not be matched but could be positively identified on high quality fin images (Q2) were given a new identification number. The majority of marked animals were adult individuals.

Demographic parameters estimation

Photo-identification data were used in mark-recapture models. Pollock's robust design with Pradel's population growth rate (Pollock, 1982; Pradel, 1996) and Huggins model (Huggins, 1989, 1991) with Random Effect (Gimenez & Choquet, 2010; White & Cooch, 2017) was used to estimate abundance (N) as a derived parameter, annual apparent survival rate (ϕ), and adult population growth rate (λ). These models are designed for long-term studies to be robust to heterogeneity with the advantage of combining open and closed population, by allowing the separation of capture events in primary and secondary sessions. Each primary period (yearly, from May to September) was separated by sufficient long intervals of time to be "open" (i.e. migration, mortality and births could occur between them). These primary sessions were divided into multiple secondary periods, each consisting of 15 consecutive days of sampling. All sightings of an individual within a secondary period were considered as one sighting.. Because the secondary sessions happened over a short period of time, they were considered "closed" (i.e. no migration, birth nor mortality). The number of secondary

97 sessions varied between 4 and 7 among years depending on the survey effort which was
98 dependent of weather conditions (Table 3). Secondary sessions were spaced by a
99 minimum of 2 days to allow mixing to occur.

100 The following assumptions were made for the robust design: (i) the population
101 was assumed closed to immigration, emigration, births, and deaths within primary
102 periods. Population closure within primary periods was tested using the software
103 CloseTest (Stanley & Burnham, 1999). Nevertheless, population closure was assumed
104 within primary sessions considering the longevity (Bloch, Lockyer, & Zachariassen,
105 1993; Verborgh et al., 2009), reproductive rate (Martin & Rothery, 1993), social
106 organization (de Stephanis, Verborgh, et al. 2008) and the highly localized distribution
107 of pilot whales in the Strait (de Stephanis, Cornulier, et al. 2008); (ii) naturally marked
108 individuals were “captured” during secondary sample occasions and assumed identified
109 without errors; for these analyses all naturally marked individuals were used, giving
110 demographic parameter estimates equivalent to well-marked individuals used in a
111 previous study by Verborgh et al. (2009); (iii) all individuals used the area during the
112 study period, but not necessarily every year (Kendall & Nichols, 1995). Problems of
113 transience (TEST 3) and trap dependence (TEST 2) were tested with the program U-
114 Care 2.3.2 (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009).

115 All models were run in MARK 9.0 (White & Burnham, 1999) and compared
116 using the Akaike Information Criterion adjusted for small samples size, AICc (Sugiura,
117 1978). The c-hat value was obtained from U-Care to take into account the dispersion of
118 data since it is not structurally possible to correct for either trap dependence or
119 transience within the framework used in this study. The choice of the best model was
120 determined by the lowest $\Delta AICc$ between any other model and the best model. Models
121 within $\Delta AICc \leq 2$ were considered to be well supported by the data (Burnham &

Anderson, 2004).

Hypotheses testing and model selection

Within each primary session of the Robust Design, a Huggins with Random Effect closed population model was used to estimate capture probabilities and population size. Because heterogeneity of capture between individuals was suspected, a random effect (RE) model, which uses numerical integration to integrate out continuous, individual random differences in latent encounter probability, was used within primary sessions (Gimenez & Choquet, 2010; White & Cooch, 2017). The parameter σ_p is estimated as the standard deviation of the continuous distribution of the individual variation in the encounter probability p . Since no trap-effect was expected on the behaviour, i.e. the animals were not caught but only photographed from a distance, all re-capture probability (c) were set as equal to capture probability (p).

Model selection was divided into three steps (see Table 1): (I) six hypotheses on the capture probability: M_0 , M_t , M_{RE} , M_{tRE} and a combination of $M_t + M_{tRE}$ based on the results obtained from CloseTest were tested to estimate the abundance. The effect of photographic effort was tested using the standardized number of fin images analysed in Q1 and Q2 per year as a covariate named effort. During this first step, survival rate (ϕ) and population growth-rate (λ) were left as time-dependent. The resulting best model (i.e. most parsimonious corresponding to the lowest AICc) was then used to estimate the parameters ϕ and λ . A combination of the hypotheses described in Table 1 was tested to (II) design the best model fitting the survival rate. From this new best model, (III) sex information available for 20 females and 35 males biopsy sampled in 2006 from de Stephanis, Verborgh, et al. (2008) was incorporated to test for a possible

sex-dependent effect on survival rate. For these animals, survival rate was fixed at 1 until 2006 when they were sampled alive. When two models have a delta AICc < 2, MARK allows for a model averaging of their parameters based on their AICc weights.

Abundance estimates

The abundance estimate obtained from mark-recapture models gives an estimate only for marked individuals in the population (N) for each year. Therefore, to estimate the total population size (N'), (N) must be corrected by calculating the proportion of marked individuals in the population (P). This proportion is calculated as the number of fin images of good (Q1) and high quality (Q2) of marked individuals divided by the total number (n) of fin images analysed of Q1 and Q2 quality of both marked and unmarked animals, and taken at an angle of 270° exclusively (allowing best identification). The proportion of unmarked individuals and the corrected abundance (N') were calculated for each year from 1999 to 2011. The variance of P is taken into account through its coefficient of variation ($CV(P)$) calculated in equation 1:

$$\text{Equation 1: } CV(P) = \sqrt{\frac{P(1-P)}{n}} / P$$

Upper and lower bounds of 95% confidence intervals for the total estimation of the population abundance (UCI(N') and LCI(N') respectively) were calculated according to the formula used by Whitehead, Gowans, Faucher, & McCarrey (1997) in Equation 2:

$$\text{Equation 2: } LCI(N') = N' \times (1 - 2 \times \sqrt{\left(\frac{N - LCI(N)}{2N}\right)^2 + CV(P)^2})$$

$$UCI(N') = N' \times (1 + 2 \times \sqrt{\left(\frac{UCI(N)-N}{2N}\right)^2 + CV(P)^2})$$

where $LCI(N)$ and $UCI(N)$ are the 95% confidence intervals estimated for the abundance of the marked individuals (N).

Mark-recapture models rely on the correct identification of individuals and in this study, most naturally marked animals were adult individuals as young animals were often unmarked. While we believe that the correction factor significantly decreases a possible bias in total abundance estimates by taking into account unmarked individuals including young animals, calf and juvenile survival could have been affected differently than adult's and was not assessed in this study. Indeed, survival rates are generally lower for immature marine mammals (Bloch et al., 1993), and the death of a mother could have direct consequences on the survival of her offspring, both at young age, and even for adult descendants as found in killer whales (Foster et al., 2012). However, stranding data indicate that mainly adult and subadult individuals were affected (Fernández et al., 2008) and therefore the estimated parameters should reflect how the epizootic affected these age classes in the population.

The number of dead individuals before and during the winter 2006-2007 was estimated by multiplying the apparent annual survival rate by the total population estimate the same year and its lower and upper confidence interval limits. This estimate can then be compared with the average of 0.9 strandings per year between 1998 and September 2006 and the 10 individuals that were recorded stranded between October 2006 and February 2007 in the Strait of Gibraltar (Fernández et al., 2008) to calculate the proportion of apparently dead individuals that stranded.

Results

From 1999 to 2011, 301 sightings of pilot whales, corresponding to 221 sampling days in the Strait of Gibraltar, were used in this study. A total of 55,336 pilot whales' dorsal fin images of good and high quality (Q1 and Q2) were used for the analyses, resulting in the identification of 360 individuals. The photographic effort and fin image quality increased through the study period (Figure 1).

The annual discovery rate of new individuals identified varied between years, and three periods of large increases were observed in 2004, 2007 and 2010 (Figure 2A). The annual number of total identified and resighted individuals increased from 1999 to 2006 and reached a maximum of 96% of resighted individuals in 2008. The average annual resighting rate was 77% (95% CI: 66.8%-87.0%) over the study period (Figure 2A). The quantity and quality of fin images analysed have increased over the years, thus increasing the probability to identify the individuals present in the area (Figure 1). The high value in 2004 corresponds mainly to the switch to a digital camera system which increased the quality and quantity of photographs obtained. Although, the effect of photographic effort on capture probability did not improve the model (Table 2), a general increase in capture probability was still observed in the dataset (Table 3). Low capture probability would inflate the estimate of population abundance and increase the uncertainty around the estimates of survival and population growth rate. The increases of new individuals identified in 2007 and 2010 can be explained by the entrance of previously unknown social groups in the area (de Stephanis, Verborgh, et al. 2008), and biological recruitment.

Population closure hypothesis (Stanley & Burnham, 1999) was only met ($p < 0.05$) in the first 6 of the 13 years (1999-2004). However, after comparing the

population estimates between open robust design and closed population robust design with heterogeneity, the population estimates were similar without, and higher, taking into account heterogeneity for the years 2005-2011 (data not shown). Therefore closed population models with heterogeneity were used for the remaining of the analyses (Wilson, Hammond, & Thompson, 1999). Transience and trap dependence (trap-happiness) were also detected in the dataset ($X^2=236.19$; $df=47$; $p=0$) which $\hat{c}$ (5.03) was used to correct for overdispersion of the data.

The best model, with all the individuals pooled together, had a constant apparent survival rate before the epizootic, a lower value the year of the epizootic and constant again after; additionally both population growth rate and capture probability were time dependent, the latter taking into account individual heterogeneity for the years 2005-2011 (Model 1 in Table 2 and Figure 2C). Finally, a model averaging of the two best models (within 2 AICc) showed slightly lower apparent survival rates for males than for females from 2006 onwards (Model 2 in Table 2 and Figure 2C). The apparent annual survival rate of the population was estimated at 0.984 (SE: 0.005; 95% CI: 0.971-0.991) from 1999 to 2005, before the morbillivirus epizootic. In 2006, a similar epizootic effect was found for males and pooled sexes around 0.79, and slightly higher at 0.83 for females (Figure 2C), which stayed higher than males afterwards.

In the meantime, the proportion of marked individuals (P) ranged from 53 to 79% between 1999 and 2011 (Table 3). Both estimates of marked animals (N) and total corrected abundance (N') increased between 1999 and 2006. Then a general decrease was observed until 2011 except for 2010 (Table 3 and Figure 2B). The capture probability was generally low from 1999 until 2003 ($p=0.12$) and increased during the next period from 2004 until 2011 ($p=0.38$) (Table 3). Out of the estimated 67 (range 51-87) missing animals between 2006 and 2007, only 14.8% (range: 11.5-19.7%) were

found stranded on the Spanish coast in the Strait of Gibraltar area in 2006-07. This proportion is lower but within the range of the previous period with a mean of 20.8% (range: 10- 45%) based on an average of 4 individuals missing per year (range: 2- 9).

The estimated population growth rate was positive before 2006 ($\lambda > 1$) (Figure 2D). During the epizootic and until 2009, it was negative. It then was briefly positive again in 2010. In 2011, $\lambda < 1$ suggested another loss of individuals in the population similar to the epizootic year.

Discussion

In this study we detected a lasting Morbillivirus effect on the population of long-finned pilot whales in the Strait of Gibraltar.

The population size estimate increased between 1999 and 2006, along with a positive population growth rate and a high apparent survival rate within the range of normal values for adults of this species in other regions (Martin & Rothery, 1993; Wierucka et al., 2014). Then, in 2006 apparent survival rate declined and population growth rate became negative. Overall apparent survival was strongly affected, decreasing from 0.984 (95% CI: 0.971-0.991) to 0.788 (95% CI: 0.727-0.839), although females were slightly less affected than males (Figure 2C). The observed decline is likely related to the epizootic considering the large increase of morbillivirus-positive strandings observed during the same period (Fernández et al., 2008). Moreover, the survival rate decrease was similar to what was estimated for some social clusters (27%) of the neighbouring Alboran Sea pilot whales (Wierucka et al., 2014), although there, it did not affect the entire population. Singer, Zeigenfuss, & Spicer, (2001) suggested that a terrestrial mammal population larger than 250 individuals with a large home range, and migratory movements, i.e. with a large carrying capacity, is more likely to recover

rapidly after an epizootic. The Alboran Sea pilot whales meet these characteristics (Cañadas & Sagarminaga, 2000; Verborgh et al., 2016; Wierucka et al., 2014). They could therefore be less impacted and may recover more rapidly than the animals from the Strait, if the same logic applies to this species. In contrast, survival and population growth rate in the Strait were still lower five years after the epizootic than they were before.

Worldwide, CeMV epizootics caused higher stranding rates over a few months locally but could last for years when the virus was transmitted over larger areas (Van Bresse et al., 2014). However, results found in this study and in the nearby Alboran Sea (Wierucka et al., 2014) show that the effects, whether direct or indirect, can span over at least five years. Cumulative effects of some of the following hypotheses could potentially explain these results:

(1) A post-epizootic chronic effect of the *Morbillivirus* as reported for infected individual striped dolphins in the Spanish Mediterranean coast four years after the epizootics (Domingo et al., 1995; Soto et al., 2011).

(2) High immunosuppressive contaminant levels such as PCBs and DDTs and high biomarker responses (CYP1A1 and CYP2B) (Lauriano, Di Guardo, Marsili, Maltese, & Fossi, 2014). The levels encountered could induce viral and non-viral pathogens to take advantage and thereby enhance the epizootic effect and cause other ‘opportunistic’ infections (Lauriano et al., 2014). Furthermore, a lower survival rate was observed for adult males, which could be due to higher contaminant levels, as adult females can discharge part of their contaminant load through lactation (Borrell, Bloch, & Desportes, 1995). The sex-specific response found here differs from the similar effect observed in both sexes of all age classes in striped dolphins during two epizootics in the

Mediterranean Sea (Aguilar & Raga, 1993; Keck et al., 2010; Soto et al., 2011) which is probably explained by the use of adults in our analyses.

(3) A new epizootic in 2011 or the beginning of the endemic presence of the virus in Mediterranean striped dolphins as suggested by Rubio-Guerri et al. (2013, 2018) which could be transmitted to pilot whales (Fernández et al., 2008). Although no CeMV were detected in the few necropsies done on fresh stranded pilot whales in the South coast of Spain, it also coincides with another peak of pilot whale strandings in that area in 2011 (Consejería de Medio Ambiente y Ordenación del Territorio, 2014).

(4) An increase in shipping activity and interaction with whale watching boats in the Strait which could increase stress (Senigaglia, de Stephanis, Verborgh, & Lusseau, 2012). Stress can lower immune response and make the animals more vulnerable to infectious pathogens (Biondi & Zannino, 1997; Cohen & Williamson, 1991), such as a resurgence of CeMV, which can in turn affect their survival or reproductive rates (Ferin, 2004; Sheriff, Krebs, & Boonstra, 2009).

(5) A social network disruption due to the disease outbreak (Guimarães et al., 2007) or the removal of key social individuals (Williams & Lusseau, 2006) that would lead to higher mortalities at the population level by a chain reaction effect (Wade, Reeves, & Mesnick, 2012). Moreover, if a key individual was female, it could increase the mortality of all her offspring as observed in killer whales (Foster et al., 2012), a species with similar social structure (de Stephanis, Verborgh, et al. 2008).

(6) A natural regulator to slow down the growth of the population when it reaches carrying capacity (Van Bressem, Van Waerebeek, & Raga, 1999). The population had been growing until 2006, including a high number of newborn animals in summer 2006 with 23 newborns photo-identified, using foetal folds spacing and location on the body,

compared to 10 and 11 in 2004 and 2005 respectively, and may have reached the carrying capacity of the area. The entrance of new social groups in the area after the epizootic suggests that these groups could either occupy the ecological niche left by the victims of the epizootic or, try to increase their reproductive rate by reproducing over larger areas as observed in other species after an epizootic (Singer, Zeigenfuss, & Spicer, 2001).

(7) The apparent survival rate does not distinguish between mortality and permanent emigration. Therefore, the new social groups that have been observed some years may have never come back, or not been observed, which would decrease the apparent survival rate after the epizootic. However, members of all the resident social groups identified by de Stephanis, Verborgh, et al. (2008) were still observed in the Strait in 2011, suggesting that it is more likely that new social groups emigrated back from where they came than resident individuals left the area.

Only 14.9% of missing individuals were found stranded, which is of special interest for conservation as it helps in the assessment of the ratio of stranded vs. apparently dead animals. It falls between the 2% (range: 0-6.2%) estimated for 14 cetacean species in the Gulf of Mexico (Williams et al., 2011) and the 28% estimated for coastal bottlenose dolphins in Sarasota Bay (Wells et al., 2015). The proximity to the coast in our study is an important factor, although local strong surface currents could rapidly take a dead or weak animal out of the study area. This finding further highlights the importance of combining efforts between at-sea monitoring and stranding networks.

The impact of one, and maybe two, epizootics observed in the Strait could cause future declines in the local population, with larger mortalities than expected solely from the epizootic outbreak, probably due to different factors acting together. The population

size decrease between 2006 and 2011 and the lower apparent survival rates after the epizootic caused changes in this small resident population. Although some cetacean species that were hunted to low levels are recovering nowadays, other species that inhabit high human-impacted habitats show little or no signs of recovery (Magera, Mills Flemming, Kaschner, Christensen, & Lotze, 2013). Robust population viability analysis should be performed, but our results could indicate a risk of population decrease over the next decades. This is especially of concern as recruitment is probably limited by high levels of hormone disruptive contaminants (Lauriano et al., 2014) and habitat quality is continuously degrading through the ever growing maritime traffic and whale watching activity targeting this species (Elejabeitia, Urquiola, Verborgh, & de Stephanis, 2012) in the area. The Spanish Mediterranean long-finned pilot whale population is already considered Vulnerable by the Spanish Catalogue of Endangered Species since 2011, but the severity and duration of the decline in the Strait of Gibraltar might require that the local population be considered Endangered according to several criteria (Verborgh et al., 2016). Additionally, assessing the effect of the epizootics for immature age classes is necessary to fully understand the situation of this small population.

Epizootics are expected to increase in marine ecosystems in the future, partly due to climate change (Burge et al., 2014). Our results suggest that large mortalities result from epizootics and could have cascading effects in social animals living in high anthropogenic stressed areas. Therefore, taking adaptive management approaches would increase the resilience of ocean systems vulnerable to marine diseases in a changing climate (Burge et al., 2014). The methods typically used on land to manage virus outbreaks such as quarantining, culling, and vaccinating are not realistically adaptable in the ocean. Therefore, better understanding and predicting the conditions that lead to

outbreaks and designing ways to influence these conditions may be the best way to manage marine diseases (Burge et al., 2014). In this respect, dedicated monitoring plans to improve baseline data from long-term studies on marine health are needed. Furthermore, studies of the effect of cumulative stressors on this population would also help to quantify the effect of each one and therefore choose an appropriate course of action. For example, should maritime traffic and/or whale watching activity increase or not comply with current legislation, then they could become important stressors and would require the implementation of specific measures at the national or even international level through the International Maritime Organization (IMO).

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Table 1. Summary of the hypotheses tested on the capture probability (p) to estimate the abundance (N) and of the hypotheses tested to model apparent survival rate (ϕ) and population growth rate (λ) of long-finned pilot whales in the Strait of Gibraltar.

Step	Notation	Parameter	Description
I	M0	p	Constant capture probability without heterogeneity
	Mt	p	Time varying capture probability without heterogeneity
	MRE	p, sigmap	Constant capture probability with heterogeneity
	MtRE	p, sigmap	Time varying capture probability with heterogeneity
	Effort	p	Standardized annual photographic effort
II	t	ϕ, λ	Time-dependent
	.	ϕ	Constant through time
	Pre	ϕ	Before the <i>Morbillivirus</i> , from 1999 to 2005
	MV	ϕ	During the <i>Morbillivirus</i> , 2006
	Post	ϕ	After the <i>Morbillivirus</i> , from 2007 to 2010
III	M, F, U	ϕ	Male, Female, Unknown sex

Table 2. Results from Pradel's robust design models, with capture probability (p), abundance (N), apparent survival rate (ϕ) and population growth rate (λ). AICc weight is used for model averaging. NP is the number of parameters used in the model. The most parsimonious model is the one with the smallest AICc value.

Step	Nº	Model	AICc	Delta AICc	AICc Weight	NP	Deviance
II	1	$\{\phi(\text{Pre}(\cdot)+\text{MV}+\text{Post}(\cdot)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2843.1	0.0	0.32	81	1963.5
III	2	$\{\phi(\text{U Pre}(\cdot)+\text{MV}+\text{Post}(\cdot) M(\cdot) F(\cdot)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2844.7	1.6	0.15	85	1956.7
III	3	$\{\phi(\text{U Pre}(\cdot)+\text{MV}+\text{Post}(\cdot) M(\cdot) F(t)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2846.6	3.5	0.06	86	1956.6
II	4	$\{\phi(\text{Pre}=\text{Post}+\text{MV}) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2848.1	5.0	0.03	80	1970.6
III	5	$\{\phi(\text{U Pre}(\cdot)+\text{MV}+\text{Post}(\cdot) M(t) F(\cdot)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2848.5	5.4	0.02	87	1956.4
II	6	$\{\phi(\text{Pre}(\cdot)+\text{MV}+\text{Post}(t) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2849.1	5.9	0.02	84	1963.2
II	7	$\{\phi(\cdot) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2855.1	12.0	0.00	79	1979.7
III	8	$\{\phi(\text{U Pre}(\cdot)+\text{MV}+\text{Post}(t) M(t) F(t)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2859.8	16.7	0.00	94	1952.9
I	9	$\{\phi(t) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2860.8	17.6	0.00	90	1962.3
III	10	$\{\phi(\text{U}(t) M(t) F(t)) \lambda(t) N(\text{Mt}+\text{MtRE})\}$	2862.9	19.7	0.00	96	1951.7
I	11	$\{\phi(t) \lambda(t) N(\text{Mt}+\text{MtRE}+\text{Effort})\}$	2869.2	26.0	0.00	94	1962.3
I	12	$\{\phi(t) \lambda(t) N(\text{MtRE})\}$	2873.2	30.1	0.00	96	1962.1
I	13	$\{\phi(t) \lambda(t) N(\text{Mt})\}$	2960.6	117.5	0.00	83	2076.8
I	14	$\{\phi(t) \lambda(t) N(\text{MRE})\}$	2996.1	153.0	0.00	50	2180.8
I	15	$\{\phi(t) \lambda(t) N(\text{M0})\}$	3051.3	208.1	0.00	37	2262.6

Table 3. Population abundance estimates of marked individuals (N) per year with 95% confidence intervals (CI), coefficient of variation of abundance estimates (CV(N)), proportion of marked individuals (P in %), the number of secondary sessions used in the models and the average capture probability.

Year	N	95% CI	CV(N)	P (%)	Nb of secondary sessions	Capture probability
1999	120	89-183	0.19	69	5	0.12
2000	149	109-219	0.18	53	4	0.10
2001	175	123-263	0.20	61	4	0.08
2002	158	129-204	0.12	65	3	0.19
2003	168	138-213	0.11	67	5	0.12
2004	230	206-266	0.07	74	4	0.23
2005	243	223-274	0.05	76	4	0.33
2006	234	220-257	0.04	74	5	0.35
2007	215	210-226	0.02	74	4	0.52
2008	210	195-234	0.05	73	5	0.36
2009	198	178-229	0.06	75	5	0.36
2010	239	228-258	0.03	72	6	0.41
2011	224	203-256	0.06	79	5	0.31

Figure 1. Photographic effort per year represented as number of long-finned pilot whale fin images analyzed per quality of pictures (Q1=good in grey, Q2=high in black).

Figure 2. Demographic parameters of long-finned pilot whales in the Strait of Gibraltar between 1999 and 2011. A. Annual number of newly marked individuals identified (lines), resighted individuals (plain color). B. Corrected abundance estimates (N') with 95% confidence interval (CI) bars. C. Survival rate estimates of all individuals, males and females with 95% CI bars. D. Annual population growth rate estimates with 95% CI bars. The dashed line at value 1 means that the number of individuals recruited in the population (births and immigration) is equal to the number of lost individuals (deaths and emigrations).