

RESEARCH ARTICLE

Epizootic effect and aftermath in a pilot whale population

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European Commission, Grant/Award Number: LIFE02NAT/E/8610; Fundación Biodiversidad; Loro Parque Foundation; Ministerio de Medio Ambiente, Spain; CEPESA; Loro Parque Foundation; LIFE 'Conservación de cetáceos y tortugas de Murcia y Andalucía', Grant/Award Number: LIFE02NAT/E/8610; Ministerio de Medio Ambiente, Fundación Biodiversidad; CIRCE volunteers

Abstract

1. Over the last three decades, emerging infectious diseases have resulted in 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, and their habitat is threatened by increasing anthropogenic stress.

KEYWORDS

disease, mammals, modelling, monitoring, ocean, pollution

1 | INTRODUCTION

Disease 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 harbour seals (*Phoca vitulina*) that have gone through two phocine distemper virus epizootics causing between 50 and 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 Bresse, 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 Bresse et al., 2014), and the demographic effect on live populations is rarely known (Van Bresse et al., 2014). Over the winter of 2006–2007 the stranding rate of long-finned pilot whales along the Strait of Gibraltar coast increased 10-fold and was linked to a CeMV epizootic that 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 whale 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. 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 5 years after the epizootic.

2 | METHODS

2.1 | 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 session 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 on 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.

2.2 | 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 the Huggins model (Huggins, 1989, 1991) with random effect (Gimenez & Choquet, 2010; White & Cooch, 2017) were 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 populations by allowing the separation of capture events in primary and secondary sessions. Each primary period (yearly, from May to September) was separated by sufficiently 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 or mortality). The number of secondary sessions varied between four and seven among years depending on the survey effort, which was dependent on weather conditions (see Table 3). Secondary sessions were spaced by a minimum of two days to allow mixing to occur.

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

All models were run in MARK 9.0 (White & Burnham, 1999) and compared using the Akaike information criterion adjusted for small samples size (AICc; Sugiura, 1978). The c -hat value was obtained from U-Care to take into account the dispersion of data, since it is not structurally possible to correct for either trap dependence or transience within the framework used in this study. The choice of the best model was determined by the lowest Δ AICc between any other model and the best model. Models within Δ AICc ≤ 2 were considered to be well supported by the data (Burnham & Anderson, 2004).

2.3 | 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 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 recapture probabilities c were set as equal to capture probability p .

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

Model selection was divided into three steps (see Table 1). Step I: six hypotheses on the capture probability—M0, Mt, MRE, MtRE and a combination of Mt + MtRE 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 . In step II, a combination of the hypotheses described in Table 1 was tested to design the best model fitting the survival rate. Step III: from this new best model, sex information available from biopsies for 20 females and 35 males sampled in 2006 by 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 $\Delta\text{AICc} < 2$, MARK allows for a model averaging of their parameters based on their AICc weights.

2.4 | 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 quality (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 $\text{CV}(P)$ calculated as follows:

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

Upper and lower bounds of 95% confidence intervals (CIs) for the total estimation of the population abundance, $\text{UCI}(N')$ and $\text{LCI}(N')$ respectively, were calculated according to the formula used by Whitehead, Gowans, Faucher, and McCarrey (1997):

$$\begin{aligned} \text{LCI}(N') &= N' \left[1 - 2\sqrt{\left(\frac{N - \text{LCI}(N)}{2N}\right)^2 + \text{CV}(P)^2} \right] \\ \text{UCI}(N') &= N' \left[1 + 2\sqrt{\left(\frac{\text{UCI}(N) - N}{2N}\right)^2 + \text{CV}(P)^2} \right] \end{aligned} \quad (2)$$

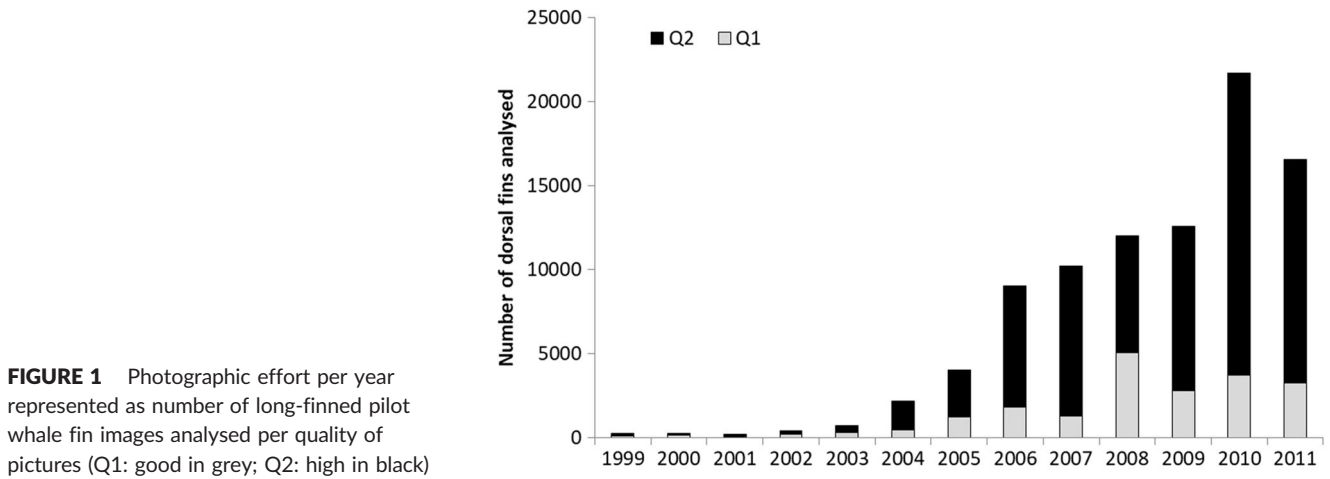
where $\text{LCI}(N)$ and $\text{UCI}(N)$ are the 95% CIs estimated for the abundance of the marked individuals N .

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. Although 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 to that of adults 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 of 2006–2007 was estimated by multiplying the apparent annual survival rate by the total population estimate the same year and its lower and upper CI 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.

3 | 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 of identifying 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

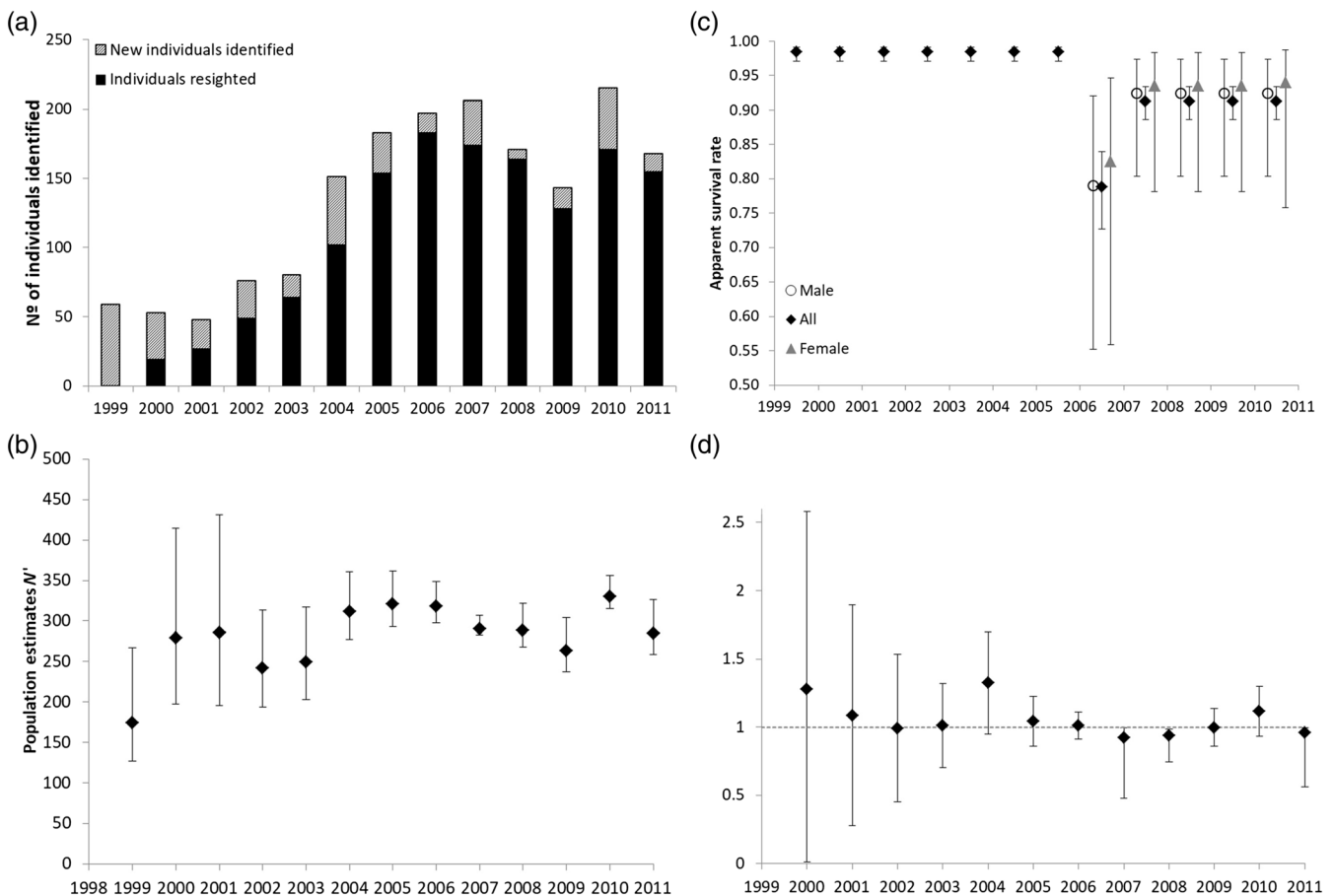


FIGURE 2 Demographic parameters of long-finned pilot whales in the Strait of Gibraltar between 1999 and 2011. (a) Annual number of newly marked individuals identified (lines), resighted individuals (black). (b) Corrected abundance estimates N' with 95% confidence interval (CI) bars. (c) Survival rate 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)

TABLE 2 Results from Pradel's robust design models, with capture probability p , abundance N , apparent survival rate ϕ and population growth rate λ . Akaike information criterion adjusted for small samples size (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	N°	Model	AICc	Δ AICc	AICc Weight	NP	Deviance
II	1	{ ϕ (Pre(.)) + MV + Post(.)) $\lambda(t)$ N (Mt + MtRE)}	2,843.1	0.0	0.32	81	1,963.5
III	2	{ ϕ (U Pre(.) + MV + Post(.)) M(.) F(.)) $\lambda(t)$ N (Mt + MtRE)}	2,844.7	1.6	0.15	85	1,956.7
III	3	{ ϕ (U Pre(.) + MV + Post(.)) M(.) F(t)) $\lambda(t)$ N (Mt + MtRE)}	2,846.6	3.5	0.06	86	1,956.6
II	4	{ ϕ (Pre = Post+MV) $\lambda(t)$ N (Mt + MtRE)}	2,848.1	5.0	0.03	80	1,970.6
III	5	{ ϕ (U Pre(.) + MV + Post(.)) M(t) F(.)) $\lambda(t)$ N (Mt + MtRE)}	2,848.5	5.4	0.02	87	1,956.4
II	6	{ ϕ (Pre(.)) + MV + Post(t) $\lambda(t)$ N (Mt + MtRE)}	2,849.1	5.9	0.02	84	1,963.2
II	7	{ ϕ (.) $\lambda(t)$ N (Mt + MtRE)}	2,855.1	12.0	0.00	79	1,979.7
III	8	{ ϕ (U Pre(.) + MV + Post(t) M(t) F(t)) $\lambda(t)$ N (Mt + MtRE)}	2,859.8	16.7	0.00	94	1,952.9
I	9	{ ϕ (t) $\lambda(t)$ N (Mt + MtRE)}	2,860.8	17.6	0.00	90	1,962.3
III	10	{ ϕ (U(t) M(t) F(t)) $\lambda(t)$ N (Mt + MtRE)}	2,862.9	19.7	0.00	96	1,951.7
I	11	{ ϕ (t) $\lambda(t)$ N (Mt + MtRE+Effort)}	2,869.2	26.0	0.00	94	1,962.3
I	12	{ ϕ (t) $\lambda(t)$ N (MtRE)}	2,873.2	30.1	0.00	96	1,962.1
I	13	{ ϕ (t) $\lambda(t)$ N (Mt)}	2,960.6	117.5	0.00	83	2,076.8
I	14	{ ϕ (t) $\lambda(t)$ N (MRE)}	2,996.1	153.0	0.00	50	2,180.8
I	15	{ ϕ (t) $\lambda(t)$ N (MO)}	3,051.3	208.1	0.00	37	2,262.6

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

Year	N	95% CI	$CV(N)$	P (%)	No. 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

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 into 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 six 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 analyses (Wilson, Hammond, & Thompson, 1999). Transience and trap dependence (trap-happiness) were also detected in the dataset ($\chi^2 = 236.19$; $df = 47$; $p = 0$), where c -hat (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 2AICc) 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 with an apparent annual survival rate of 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 four 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.

4 | 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, and 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 5 years after the epizootic than they were before.

Worldwide, CeMV epizootics have caused higher stranding rates over a few months locally but could last for years when the virus was transmitted over larger areas (Van Bresseem 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 5 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 4 years after the epizootics (Domingo et al., 1995; Soto et al., 2011).
2. High immunosuppressive contaminant levels, such as polychlorinated biphenyls and dichlorodiphenyltrichloroethanes 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 was detected in the few necropsies done on fresh stranded pilot whales on 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 Bresseem, 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 fetal folds spacing and location on the body, compared with 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 et al., 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 versus 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 or 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 anthropogenically 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.

ACKNOWLEDGEMENTS

We would like to thank CIRCE volunteers, research assistants and staff that helped in the field work and abled this long-term monitoring of pilot whales. This work was funded by the Ministerio de Medio Ambiente, Fundación Biodiversidad, LIFE 'Conservación de cetáceos y tortugas de Murcia y Andalucía' (LIFE02NAT/E/8610), Loro Parque Foundation and CEPSA. Thank you also to the editor and two anonymous reviewers who greatly improved the manuscript. The authors have no conflict of interest.

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How to cite this article: Verborgh P, Gauffier P, Brévert C, et al. Epizootic effect and aftermath in a pilot whale population. *Aquatic Conserv: Mar Freshw Ecosyst*. 2019;29:820–828. <https://doi.org/10.1002/aqc.3082>