



Sharp decreases in survival probabilities in the long-finned pilot whales in Strait of Gibraltar

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Abstract

The Strait of Gibraltar has some of the highest maritime activity in the world. Its populations of cetaceans are threatened by noise, chemical pollution, and collisions by the many boats crossing the strait. One of the greatest threats identified in cetaceans in the Mediterranean are epizootics that severely affect the most sensitive vital rate in long-lived species: adult survival. By a multi-event analysis of a 16-year database of long-finned pilot whale photo identification capture–recapture data, we analysed adult survival in the Strait of Gibraltar’s resident population and evaluated the possible effects of epizootics on this vital rate. We identified the large effect of a morbillivirus epizootic that occurred in 2006–2007, but we also revealed a second collapse in survival in 2011, probably due to another morbillivirus epizootic. These episodes seem to affect sexes differently, with females being less affected than males. Interestingly, the morbillivirus epizootic not only sharply decreased survival after the episode, but the effect extended over time, probably showing post-epizootic sequelae. These disease outbreaks have increased during the last decades worldwide and could be linked to anthropogenic threats such as organochlorine contamination. This may explain the high frequency of epizootics in the Gibraltar area. We warn about the conservation status of this long-finned pilot whale population and recommend the application of measures to reduce contamination on this nutrient-rich area to improve conditions for many marine species inhabiting this area.

Keywords Cetaceans · Strait of Gibraltar · Epizootic · Adult survival · Multi-event · Morbillivirus

Introduction

The Strait of Gibraltar is the natural connection between the Mediterranean Sea and the east Atlantic Ocean. A pulsed upwelling induced by the tides and constrained by the bathymetry (Echevarría et al. 2002) provides a nutrient-rich

water in the area. This nutrient-rich zone is also one of the areas with the highest human marine activities in the world, resulting in many different anthropogenic threats for many marine species inhabiting the area. The maritime traffic has increased by 41% between 2001 and 2010 when 116 000 vessels (over 50 m and 200 tons) were recorded crossing the Strait excluding other activities, such as fishing, sailing and whale watching) (Tenan et al. 2020).

This high concentration of nutrients in the area allows the residency of many marine species among them, six species of cetaceans (Cañadas et al. 2005; Guinet et al. 2007; de Stephanis et al. 2008a). One of these resident species is the long-finned pilot whale, *Globicephala melas* (de Stephanis et al. 2008a). The matrilineal long-finned pilot whale is divided into two subspecies, one in the temperate seas of the Southern Hemisphere and the other restricted to the North Atlantic Ocean and Mediterranean, and a strong genetic differentiation is observed between the North Atlantic and Mediterranean populations (Kraft et al. 2020). Long-finned pilot whales are protected in the ACCOBAMS agreement (<http://www.accobams.org/>); however, their conservation

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status in IUCN red list is still not determined for the species in the Mediterranean because “appropriate data are not available on the species biology, distribution and abundance in the Mediterranean” (Minton et al. 2018). Human activities that may threaten pilot whales, as well as other marine species include, noise pollution, collision, or the accumulation of chemical pollution through trophic chain (Bustamante et al. 1998). Levels of contamination of certain chemical substances such as organochlorines (OC’s) in the pilot whale’s Mediterranean population are between 5 and 10 times higher than in the population of Atlantic North (Praca et al. 2011; Lauriano et al. 2014; Dam and Block 2000).

Another important threat identified for the species in the Mediterranean are epizootics, mainly by the dolphin morbillivirus (DMV), a strain first isolated from Mediterranean striped dolphins (*Stenella coeruleoalba*) (Domingo et al. 1990). Infectious disease emergence has increased significantly over the last 30 years, with mass mortality events (MMEs) associated with epizootics becoming increasingly common (Gulland et al. 2007; Sanderson and Alexander 2020), generating conservation concerns not only at the species level, but also at the ecosystem level (Behringer et al. 2020). In the Mediterranean, due to the specific DMV morbillivirus strain, two well-documented epizootics have been registered. The first one in 1990–1992 produced outbreaks of mass mortality in the striped dolphin and is suspected to have also affected other cetacean species, such as pilot whales, but little is known about the impacts on other cetacean species (Van Bressemer et al. 2014). The second DMV epizootic occurred in 2006–2007, and again severely affected several cetacean species, including pilot whales at the Gibraltar Strait (Fernández et al. 2008; Van Bressemer et al. 2014). Both epizootics are believed to have begun in or close to the Strait of Gibraltar (Van Bressemer et al. 2014) and it was suggested that pilot whales possibly transmitted the infection to the striped dolphins with which they occasionally form mixed groups (Raga et al. pers. observations). In 2011, an unusual mass mortality episode in striped dolphins occurred in the Western Mediterranean and DMV was also postulated as the possible cause of the die-offs (Rubio-Guerri et al. 2013). Two adults striped dolphins were found stranded on the southwestern coast of Spain close to Gibraltar in 2011 and 2012 with systemic morbillivirus infection (Soto 2014). This episode overlapped in time with an increase in pilot whale stranding reported in southern Spain (11 in 2011, against 2 in 2010) (Consejería de Medio Ambiente y Ordenación del Territorio 2014). However, the only necropsy done on the stranded pilot whales was negative to morbillivirus. As predicted by life history theory, population dynamics of long-lived species are mainly driven by adult survival (Stearns 1992; Caswell 2001); thus, a decrease on this vital rate is critical for the conservation of these species. Previous studies analysed survival in this population and

showed that survival was high and constant before the morbillivirus epizootic in 2006–2007, and severely decreased after the epizootic (Verborgh et al. 2009, 2019; Wierucka et al. 2014). However, this previous analysis was done in the multistate framework and did not correct for a transient effect (Pradel et al. 1997) or trap heterogeneity (Pradel and Sanz-Aguilar 2012). Additionally, nothing is known on the survival in this population in the last years, when pollution and traffic increased in the area and another morbillivirus epizootic is suspected to have occurred (Rubio-Guerri et al. 2013).

By a multi-event analysis of a 16-year database of long-finned pilot whale photo identification capture–recapture data, the aim of this study is to estimate survival, the most sensitive demographic parameter for this long-lived species, and to analyse and evaluate the factors affecting its variation in this species and study area, especially the effects of epizootics. Results will be useful for assessing the conservation status of this long-finned pilot whale population and for guiding future conservation policies around the area.

Materials and methods

Study species and study area

We analysed data of a population of pilot whales (*Globicephala melas*) from the Strait of Gibraltar (35° 56' N, 5° 39' W). This Strait has a length of approximately 60 km, a width spanning from 15 to 40 km, and a maximum depth of 1000 m.

Long-finned pilot whales are long-lived animals belonging to the order of *Odontoceti* and the *Delphinidae* family (Vilstrup et al. 2011) that can reach 59 years old for females and 46 years old for males (Bloch et al. 1993). Their dorsal fin is frequently marked by injuries, such as marks and notches, which allows for individual recognition. Reproduction involves 12 months of gestation and 2 years of lactation (Lockyer 1993). Prior studies in the Mediterranean Sea have shown that they are deep divers (Baird et al. 2002). Their diet is not well known, but stranded individuals contained squid beaks and fish otoliths (de Stephanis et al. 2008b).

The different populations of the Mediterranean share common ancestors, but genetic distances indicate that the Strait of Gibraltar population differs from other Mediterranean populations, showing a very low rate of recent migration (Verborgh 2015; Kraft et al. 2020).

Database

We obtained our database from a catalogue of photographs of long-finned pilot whales in the Strait of Gibraltar that identify individuals by their marks (shape, notches, and

nicks). Between 1999 and 2015, cetaceans were encountered by trained observers equipped with 7×50 mm binoculars. They searched for cetaceans with random transects at an average speed of 5.3 knots, covering 180° in front of the boat, with one-hour shifts. The left side of the dorsal fin of each animal observed was photographed as closely as possible and oriented to 270° . The left side is easier to observe because the population swims against the inflow of Atlantic surface water from the east, so by taking photos from south, the photographer gets a better light. For each photograph taken, we registered: sighting number, photo number, total number of individuals in the photo, number of the individuals analysed in the photo (starting with the nearest individual to the furthest, from left to right when individuals were at the same distance), exposure of the dorsal fin out of the water, angle, image quality, individual code in the catalogue, and the proportion of the back behind the dorsal fin out of the water. Each dorsal fin picture corresponding to these photos was qualified based on: focus, size, orientation, exposure, and percentage of visible fin on each photograph. Three categories of pictures were used: with bad quality focus and angle (Q0), medium quality clearly visible but with defects (Q1), and high quality with optimal focus and angle of 270° (Q2).

During the study period, each analysed dorsal fin picture was crossed with pictures of all previously identified individuals in the catalogue for identification, and animals that could not be recognised were added to the catalogue with a new code name.

Once the catalogue was built, we selected the adequate data to perform the demographic analysis. First, even if data were collected continuously over the study period, following the premises for capture-recapture studies, we limited data from individuals from February and October. We selected this period because more photos were taken and analysed. Second, to avoid any misidentification, we only used pictures with good quality (classified as Q1 and Q2). We incorporated data from 60 individuals previously sexed genetically (de Stephanis et al. 2008c; Verborgh 2015).

Survival analysis

As required, before any demographic analysis, we did a Goodness of fit (GOF) test to assess the fit of our data. Since there is no GOF test available for these multi-event models, we assessed the fit of a unistate model (Cormack–Jolly–Seber type models) using U-care (Choquet et al. 2009b). This software provides information on overdispersion of our data and its main sources of lack of fit. Test 2.CT points to a trap heterogeneity, i.e. successive capture events are not independent and Test 3.SR point to a transience effect, i.e. individuals captured for the first time ('new individuals') have a lower expectation of being re-observed

in the future as compared to individuals of the same sample that had been captured previously. Based on our GOF results, we then took into account the main sources of lack of fit on our model design (see "Results") and additionally corrected for the remaining lack of fit using the estimated correcting factor (\hat{c}).

To estimate demographic parameters and analyse factors affecting them, we worked on the multi-event capture–recapture framework (Pradel 2005) and used the software E-SURGE 2.1.4 (Choquet et al. 2009a) to develop the models. Multi-event models hold two levels: (1) the field observations called "events" encoded in the capture histories, and (2) the "states" defined to match the biological questions that can only be inferred. Individual histories were coded with 4 different code events: not seen (0), seen and genetically identified as male (1), seen and genetically identified as female (2), seen but unknown sex (3). As the results of the Goodness of fit test (GOF) suggested there was trap heterogeneity in our data (see "Results" below), all of our models considered two possible state transitions with different recapture probabilities, called "aware or trap aware", when it is released after marking or re-sighting and the state "unaware" or "trap unaware", which follows any occasion where it is not captured or re-sighted (Pradel and Sanz-Aguilar 2012). Thus, we defined 5 different states, coded as AAM for alive aware males, AUM for alive unaware males, AAF for alive aware females, AUF for alive unaware females, and D for dead (see Appendix S1 for details). Due to different observation efforts over the years, we suspect recapture probabilities varied with time; however, we tested for a possible constant recapture probability over time. As GOF analyses showed a transience effect (see "Results" below), all our models included two age classes when estimating survival probability, to differentiate those individuals seen for the first time from those previously seen. We developed different models assuming different effects in survival and recapture probabilities and compared the fit of them to understand variations in adult survival in this species during the study period. We tested if survival varied or was constant during the study period, and possible effects of the epizootic on this vital rate; if survival was constant but changed before and after the first epizootic, if was constant before epizootic episode and time-dependent after the first epizootic, or constant during the study period and with lower survival during the first and a potential second epizootic (between 2006 and 2007 and between 2011 and 2012). Additionally, we tested if there was a differential effect of the epizootic episodes between sexes. We first selected the structure that best fit to our data for recapture probabilities and then used this structure for analyse variation on survival probabilities. Model selection relied on QAICc, which is the Akaike Information Criterion (AIC) corrected for overdispersion and for small sample sizes (Burnham and Anderson

2002). The model with the smallest QAICc was selected as the most parsimonious (Burnham and Anderson 2002). We considered that models with a difference of 2 or less in AICc values were statistically equivalent, and strong evidence of better fit when the difference between models is more than 4 points (Burnham and Anderson 2002).

Results

Database

Between 1999 and 2015, 137,125 dorsal fin pictures of pilot whale were taken and analysed, and 452 individuals were identified. From this database, we selected 91,189 dorsal fin pictures of quality Q1 and Q2 obtained between February and October, corresponding to 446 sightings. These pictures allow us to make 66,998 identifications from 447 individuals.

Goodness of fit

The global goodness-of-fit test made with U-CARE 2.3.4 indicates there was lack of fit ($\chi^2 = 367.991$; $df = 64$; $P = 6.821e-12$). We found strong evidence of transience effect (TEST 3. SR; $\chi^2 = 104.559$; $df = 14$; $P = 6.661e-16$) and of trap happiness dependence effect (TEST 2CT; $\chi^2 = 169.504$; $df = 14$; $P = 0$). We corrected for transience by including two age classes when estimating survival probability, and trap dependence by considering two state transitions (see methods section), and corrected for the remaining over-dispersion with a variance inflation factor $\hat{c} = 2.6091$.

Survival analysis

Results clearly show that recapture probability is variable over time (Table 1). Best models explaining our data also clearly show that apparent survival was constant and high before the first epizootic episode but became time-dependent afterwards (Model 1 and 2, Table 1). Even if evidences are not conclusive (difference between models were less than 4 QAICc points), our results suggest an effect of sex on apparent adult survival (Model 1, Table 1).

The lowest survival was found after the suspected second epizootic episode (0.649 ± 0.085) (2011–2012) and the highest between 2013 and 2014 (0.994 ± 0.079) (Model 2, Table 1 and Table 3). Results of the model assuming two constant survival values, one before the epizootic and the other one after the epizootic (Model 7, Table 1) showed that before first epizootic, male apparent survival (0.994 ± 0.006) and female apparent survival (0.999 ± 0.002) were high and similar (Table 2). After the first epizootic episode in 2006, male apparent survival sharply decreased (0.829 ± 0.041), much more than female apparent survival (0.958 ± 0.029) (Model 7, Table 2).

In Fig. 1 and Table 3, we can see the impact of epizootic on adult survival. In 2006, coinciding with the first epizootic, we clearly observed a decrease on survival and between 2011 and 2012, after the suspected second epizootic, another strong decrease in survival was observed. Our results show that in both the decrease in survival extended over time, and that in 2011 survival probability decrease even more than in 2006–2007, and extended longer than in 2006 (Fig. 1, Table 3). Results show also that differences in survival may exist between sexes, with females having a higher apparent

Table 1 Model selection for estimating apparent adult survival in pilot whales in Gibraltar

Model	Survival	Recapture	np	Dev	QAICc	Δ QAICc	QAICc weight
1	t2+sex	Trap+t	32	4170.280	1663.308	.0000	0.740
2	t2	Trap+t	31	4181.191	1665.432	2.124	0.256
3	t	Trap+t	37	4172.275	1674.390	11.1082	0.003
4	t3+sex	Trap+t	27	4231.525	1676.511	13.203	0.001
5	t3	Trap+t	26	4240.896	1678.054	14.746	0.000
6	i2+sex	Trap+t	24	4271.011	1684.967	21.659	0.000
7	i2	Trap+t	23	4282.756	1687.469	24.161	0.000
8	i	Trap+t	22	4412.079	1735.487	72.179	0.000
9	t2	Trap+t	16	4449.044	1737.445	74.137	0.000

Survival and Recapture show the effects tested for the parameters. “np” is the number of parameters used in the model. Dev is the Residual Deviance of the model. QAICc is the corrected AIC for over-dispersion. Δ QAICc is the difference between QAICc’s from the model and the first model. QAICc weight gives the probability for each model in relation to the best model tested. In the analysis, we ran different models to test if survival was: constant during the study period (i), time-dependent during the study period (t), with two different constant survival probability, before and after the first epizootic (i2), constant before epizootic episode and time-dependent from 2006 to 2015 (t2), and constant during the study period except during the epizootic episodes, where survival would be time variant (i.e., time-dependent between 2006 and 2007 and between 2011 and 2012) (t3)

Table 2 Apparent survival probabilities (mean ± SD) for males and females from the best model

Sex	Before epizootic	Minimum after epizootic	Maximum after epizootic
Male	0.996 ± 0.004	0.482 ± 0.140 (2011–2012)	0.993 ± 0.030 (2012–2013)
Female	0.999 ± 0.001	0.772 ± 0.087 (2011–2012)	0.998 ± 0.009 (2012–2013)

In parenthesis the corresponding time interval

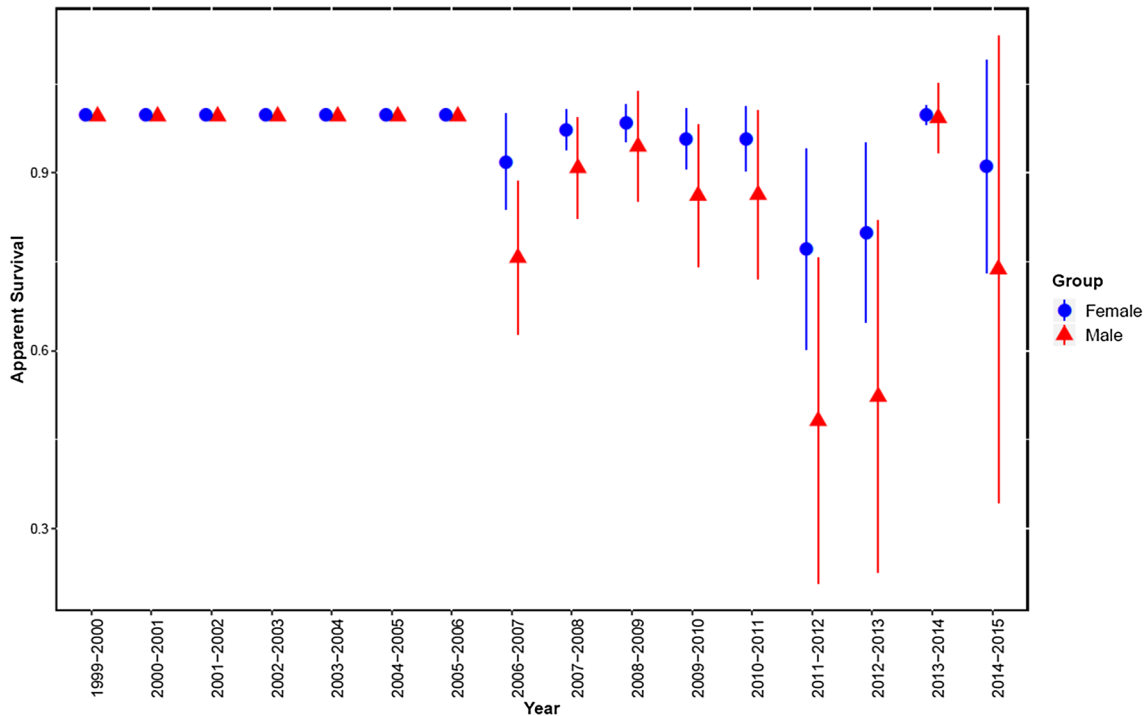


Fig. 1 Strait of Gibraltar’s pilot whale population apparent survival probability between 1999 and 2015. These estimates are from the best model. Points represent the apparent survival from Male (red trian-

gles) and Female (blue dots). The vertical lines indicate the 95% credible interval for the estimates

Table 3 Annual apparent survival probabilities (mean ± SD) from models 1 and 2 and averaged estimates from both models

Year	Model 1		Model 2	Averaged estimates	
	Male survival	Female survival	Mean survival	Male survival	Female survival
2000–2006	0.996 ± 0.004	0.999 ± 0.001	0.997 ± 0.003	0.996	0.999
2006–2007	0.757 ± 0.066	0.919 ± 0.041	0.831 ± 0.042	0.776	0.897
2007–2008	0.908 ± 0.043	0.973 ± 0.018	0.941 ± 0.026	0.916	0.965
2008–2009	0.945 ± 0.048	0.984 ± 0.016	0.965 ± 0.030	0.950	0.979
2009–2010	0.862 ± 0.062	0.958 ± 0.026	0.913 ± 0.036	0.875	0.947
2010–2011	0.863 ± 0.072	0.958 ± 0.028	0.917 ± 0.042	0.877	0.948
2011–2012	0.482 ± 0.140	0.772 ± 0.087	0.649 ± 0.085	0.524	0.741
2012–2013	0.523 ± 0.152	0.799 ± 0.077	0.696 ± 0.086	0.566	0.773
2013–2014	0.993 ± 0.030	0.998 ± 0.009	0.994 ± 0.079	0.993	0.997
2014–2015	0.738 ± 0.201	0.911 ± 0.092	0.832 ± 0.163	0.762	0.891

survival than males (Tables 1–2). Survival estimates from the last year (2014) should be taken with caution (Williams et al. 2002) due to for example nonrandom (Markovian)

temporary emigration, which can introduce severe bias, particularly at the end of the time series (terminal bias: Kendall et al. 1997).

Discussion

Multi-event modelling of a long-term capture–recapture database of long-finned pilot whales in the Strait of Gibraltar, allowed us to estimate apparent adult survival, to determine some of the most important factors driving population dynamics, and to evaluate the effects of epizootics in a cetacean species inhabiting one of the most impacted areas in the world by human activities.

Adult survival for this resident population has been estimated for the first time correcting for transience and trap dependence in our models. As previously found (Verborgh et al. 2009, 2019; Wierucka et al. 2014) and expected in a long-lived species (Stearns 1992), adult survival was high and constant before the 2006–2007 Morbillivirus epizootic. When analysing data of one unique population and without including recovery data, we cannot differentiate mortality from permanent dispersal; however, previous genetic results indicated that dispersal in this population was low and equal between sexes (Verborgh 2015). The extremely high value of adult survival estimated for both sexes in this population reinforces this previous knowledge and supports the idea that this is a resident population that permanent dispersal is usually very low, and the decrease in survival is probably due to mortality. Over the last 20 years, epizootics caused by Cetacean morbillivirus have been responsible for many die-offs in marine mammals worldwide and have caused mass mortality in several species, being a matter of concern for the conservation of many species and marine ecosystems (Gulland et al. 2007; Van Bresseem et al. 2014; Sanderson and Alexander 2020). Our results showed the large effect on survival in pilot whales at the Strait of Gibraltar of a morbillivirus epizootic in 2006–2007, but we also revealed a second collapse in survival in 2011, reinforcing the idea that in 2011 a third DMV epizootic occurred in the Mediterranean Sea that affected striped dolphins, this pilot whale population, and other cetacean species. Our results show that the last suspect outbreak in 2011 had a greater impact than the one that occurred in 2006–2007, by both a greater decrease on survival and its longer impact. However, the number of recorded strandings during 2011 was lower than that recorded during 2006–2007, which emphasises the importance of population monitoring to detect in situ mortality events.

In prior outbreaks, juveniles were those mostly affected during the mortality event in 2006–2007, likely because adults were still protected by immunity acquired during the 1990–1992 epizootic (Raga et al. 2008; Keck et al. 2010); however, we showed that adults, were also strongly affected by these episodes. Remarkably, the effect of the morbillivirus was not restricted to the epizootic episode,

but it extended over time, most likely linked to a post-epizootic sequelae of the morbillivirus, seen in other species like striped dolphin (Soto et al. 2011). After a morbillivirus infection, cetaceans can develop a chronic infection of the central nervous system (CNS), producing lesions in the brain that can be lethal (Van Bresseem et al. 2014). Additionally, being exposed to morbilliviruses has immunosuppressive effects, thus leading to secondary infections (Aznar et al. 2005).

The high mortality events affected both sexes, although males showed a more severe decrease in survival rate than females. Although females live longer than males and a difference in survival rate is expected between both sexes, the sharp decreases observed could be explained by different factors. These results would agree with the idea that high concentrations of organochlorines could affect the immune system, and females, being able to offload contaminants through pregnancy and lactation, would be less affected by the severity of infections (Aguilar and Borrell 1988). Another potential factor could be that as in killer whales, which have a similar social structure, males were shown to have higher mortality than females when their mother would die (Foster et al. 2012).

Both the 1990–1992 and 2006–2007 DMV epizootics and the suspect outbreak in 2011 started close to or in the Gibraltar Strait (Fernández et al. 2008). Gibraltar Strait may play an important role in the epidemiology of Cetacean morbillivirus. Specific environmental conditions in the area (i.e., higher water temperatures) and the fact that many individuals from several species and populations occur in the area either inhabiting there or by migration through it, may be important comingling factors that may increase the probability of Morbillivirus transmission. Moreover, outbreaks of lethal disease are usually reported in populations with decreased immunity (Van Bresseem et al. 2014). The immune status of individuals may decrease due to several natural and anthropogenic factors. One of these factors may be environmental contamination. The organochlorine contamination concentrations in blubber found in the Strait of Gibraltar pilot whale population (268.31 µg PCBs/g), exceeds by 15 times the accepted toxicity threshold in blubber of marine mammals set by Kannan et al. (2000), which might affect their reproduction and immune system (Lauriano et al. 2014). Also, a previous study showed that stranded and biopsied cetaceans of the Strait have one of the highest organochlorine polychlorinated biphenyl (PCB) concentrations in the world (Jepson et al. 2016). This high level of contamination can lead to increase virus infection and transmission and to an increased mortality rate when infected (Ross 2002; Aguilar and Borrell 1988). In the Strait of Gibraltar, high contaminant loads may exacerbate the severity of the disease and favour transmission between species (Aguilar and Borrell 1988; Van Bresseem et al. 2014). Survival rate in the

Alboran Sea long-finned pilot whale population after the 2006–2007 epizootic was higher than the one estimated at the Strait of Gibraltar population (Verborgh et al. 2016), and one possible explanation could be that both higher contaminant levels and human activities in the Strait of Gibraltar than in the Alboran Sea may aggravate the severity of the epizootic. The extension of the Tangier harbour planned for 2019, close to the main pilot whale habitat (de Stephanis et al. 2008b), may deteriorate even more the situation in the area. Additionally, epizootics causing MMEs are likely to intensify in the future, with significant consequences for marine mammal survival (Sanderson and Alexander 2020).

Our study shows the negative effects of epizootics in this cetacean species. As previously suggested (Verborgh et al. 2016), we are concerned about the actual conservation status of the long-finned pilot whale population in the Mediterranean and suggest revising its conservation classification at a local scale. Additionally, measures should be applied to reduce contamination and deterioration of this nutrient-rich area to improve conditions for so many marine species inhabiting this area.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04030-1>.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any experiments with human participants. We used published results from a previous work involving biopsy sampling that complied with the current laws of Spain and was made under the authorisation of the Spanish Ministry of Environment.

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